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## A Generic and Subgeneric Synopsis of the Male Ants of the United States

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Although not remarkably numerous in species, ants are among the most abundant of insects in individuals. Their widespread distribution, their adaptation to many types of food and environments, and their extreme activity have given them an important rank among insects that affect man's welfare. There are species that infest man's food, that bite, sting, or annoy him, gnaw into his plants or clothing, steal seeds from seed beds, remove the rubber insulation from telephone wires, kill newly hatched birds and poultry, distribute or foster other injurious insects, and possibly transmit on their bodies or otherwise the germs of such easily communicable diseases as dysentery and typhoid fever. Recently Dr. Sophie D. Griffiths, of the School of Tropical Medicine, at San Juan, Puerto Rico, has demonstrated that the fire ant, *Solenopsis geminata* (F.), which is so common in the West Indies, can carry dysentery germs on its body at least 24 hours after having crawled over infected material; and other investigators have incriminated certain species of ants as intermediate hosts in the development of internal poultry parasites. No group of insects appears to be more easily distributed by commerce than ants; thousands are intercepted each year in shipments from other countries reaching the United States by boat, plane, or other means of transportation. Moreover, the Bureau of Entomology and Plant Quarantine continually receives requests for the identification of injurious or annoying ants and for means of controlling them. As the same control measures are not applicable for all species of ants, specific determination is required before proper combative methods can be recommended. When ants are submitted for identification they may be represented by either workers, soldiers, females (queens), or males, or by any combination of these castes. The lack of adequate descriptions, and especially keys, has made the determination of males extremely difficult when specimens of this caste alone are submitted. The primary purpose of this paper, therefore, is to present a comprehensive synoptic key, supported by illustrations, for the generic and subgeneric determination of the males of the ants known to occur within the United States.

The first generic key for the identification of North American male ants was published by Cresson (1887). Although this has been of invaluable aid to taxonomists, it is now very much out of date owing to changes in nomenclature and the discovery of other genera. It includes approximately only half of the genera now recognized.

Emery in Wytsman's *Genera Insectorum* (1910, 1911, 1912, 1921, 1922, 1925) has furnished excellent keys (in French) for the generic and subgeneric determination of the male ants of the world. The keys, however, are not available to most workers and have the additional disadvantage of not being entirely applicable to the ants of the United States. In the appendix to the *Ants of the Belgian Congo*, Wheeler (1922) has offered a similar key largely adapted from that of Emery. It is primarily intended, however, for the identification of workers and females, and those sections dealing with males are not always distinctly set apart from the sections pertaining to workers and females; moreover, some genera have not been adequately treated.

That male ants have been studied so little is probably due to the fact that they are not so easily recognized as are worker ants, and also because they are present in a colony only a very short time during the course of the year. Unless males are collected in association with workers it is extremely difficult to place most of them specifically.

Males, like the other castes of ants, are distinguished from the remainder of the Hymenoptera by the presence of a pedicel, between the thorax and abdomen, which bears one or two dorsal enlargements, called nodes. When the pedicel is single-segmented, the node is called the petiole; if the pedicel is two-segmented, the two nodes are respectively known as the petiole and postpetiole. The other Hymenoptera which approach this condition can usually be distinguished from male ants by the presence of a second recurrent vein in the front wing. This vein seems to be absent in all our North American male ants, except a few of the rare Cerapachyinae.

Male ants can be distinguished from female ants by their genitalia, smaller size, and more slender form, larger eyes in proportion to the size of the head, usually much reduced or vestigial mandibles, and their 13-segmented antenna (with exceptions as noted below). Although a female ant may bear a striking resemblance to a worker of the same species, the male has a habitus so decidedly different from either that there is nothing very suggestive of relationship. In no group are the workers and males more unlike than in the legionary ants, species of *Eciton*, in which the male is unusually large and wasplike, with prominent eyes and ocelli and one-segmented petiole, whereas the worker is much smaller and has exceedingly small eyes, no ocelli, and a two-segmented petiole.

The male antenna is composed of from 10 to 13 segments, 13 being the most common number. Apparently all males belonging to the subfamilies Ponerinae, Cerapachyinae, Dorylinae, Dolichoderinae, and Formicinae have 13-segmented antennae except those of the genus *Brachymyrmex* (Formicinae). Males of Pseudomyrminae apparently always have 12-segmented antennae, while in males of Myrmicinae the number ranges from 10 to 13, although it is usually 13. The length of the male scape is so reduced in certain species that the antenna, so characteristically elbowed in the worker or female, is not at all elbowed or not noticeably so. Usually the wings are retained throughout life although some Dorylinae may lose their wings before death, and abnormal, wingless males occur in a few genera such as *Ponera*, *Anergates*, *Leptothorax*,



*Cardiocondyla*, and *Symmyrmica*. The male is distinctly workerlike in all these genera except *Anergates*, where it is distinguished by its pupoid form.

The key offered here is based on the ants of the United States. Efforts were made to obtain for study males of every species, and although this aim could not be realized it is believed that the large number of forms examined has provided a sound basis for determining the variational ranges in most genera. In some instances, especially with the rare parasitic species, it was necessary to rely upon published descriptions when no specimens were available. Since it was desired to make the keys as simple and practical as possible, no characters were used whose presence could be detected only through a great deal of laboratory preparation or technique. The keys are, therefore, largely based on external characters which are easily seen. Unfortunately, at times, some of the appendages on the gaster may be partly or entirely obscured by the strong contraction that has taken place there.

Detailed studies have shown considerable variation in wing venation, in the development of Mayrian furrows, in the relation of the length of the scape to the combined lengths of certain funicular segments, and in other characters. Not only does such variation occur in the same genus or species, but with respect to the wings it may occur in the same individual. There are specimens of *Stenamma*, for instance, with one discoidal cell in one wing and two discoidal cells in the other. Because of such variation it has often been necessary to use qualified statements and also to fortify the keys with numerous supplementary supporting characters, helpful figures, indication of approximate sizes, statements on distribution and rareness, and, finally, to furnish summaries of what are considered to be the best generic characters. It is true that the males of most genera have a distinctive habitus, but this habitus often defies accurate description. Most generic and subgeneric determinations should be comparatively easy and certain with the keys presented here. In a few genera, however, there are males with such unstable characters that considerable difficulty is encountered in attempting identification. Especial reference is made to *Stenamma* and to some species of *Leptothorax*. For accurate results every character mentioned in the key should be examined and the specimen finally checked against the generic summary. It will be noted that adequate characters have not been found for separating some of the subgenera. There seem to be no dependable characters for separating the males of the Dolichoderinae and Formicinae;\* accordingly, the genera composing them are all grouped together in a common key.

Where possible, measurements have been given of the males of the smallest and largest species in a genus to indicate range in size. Often only the male of a single species or the males of a very few species in a genus were available; hence, the measurements should be considered as only approximate. Measurements of the comparative length and breadth of the head or of the length of the scape in relation to the combined lengths of certain funicular segments

\* Forel (1874) states that the males of the Dolichoderinae in Switzerland can be separated from those of the Formicinae by the presence of pectinate spurs of the middle and hind legs and by the extension of the clypeus between the frontal carinae.

should be interpreted as follows: The length of the head is the median length from the anterior border of the clypeus to the posterior border of the head. The breadth of the head is the greatest width between the external borders of the eyes. The length of the scape with relation to the combined lengths of certain funicular segments refers to the greatest length of all these parts when fully extended. The bulblike base of the scape is not included in its length because the bulb is more or less buried in the head and therefore cannot be accurately measured.

All discussions of venation apply only to the front wing. Areas on the wing are not considered as definite cells unless completely enclosed by veins. The expression "no radial cell" may therefore mean that the area in which the radial cell should occur is entirely without veins or that, if the veins are present, they do not completely enclose the cell.

The 61 genera treated in this article are divided among the 7 subfamilies as follows: Ponerinae 11, Cerapachyinae 2, Dorylinae 1, Pseudomyrminae 1, Myrmicinae 32, Dolichoderinae 6, and Formicinae 8. Of the 726 species known to occur in the United States the Ponerinae contains 30, the Cerapachyinae 3, the Dorylinae 19, the Pseudomyrminae 5, the Myrmicinae 384, the Dolichoderinae 26, and the Formicinae 259.

Specimens used in this study are largely from the collections of the United States National Museum and that of Dr. W. M. Mann. Mr. Wm. F. Buren supplied a few specimens not otherwise available and Dr. A. C. Cole, Jr., made some helpful suggestions and criticisms of the keys. The illustrations from the "Bulletin of the American Museum of Natural History," "Biological Bulletin," and from Wheeler's "Ants" are published with the permission of Mrs. W. M. Wheeler and the editors of these publications. All the other illustrations were made by Mrs. Mary F. Benson with the exception of that of *Leptothorax diversipilosus* M. R. Smith, which was drawn by Arthur Cushman.

#### KEY TO SUBFAMILIES

1. Pedicel composed of 2 segments, the petiole and postpetiole ..... 2
- Pedicel composed of a single segment, the petiole ..... 3
2. (1) Clypeus not extending back between frontal carinae (fig. 1, E); eyes large, elongate subreniform; elongate, slender ants; antenna 12-segmented; no Mayrian furrows; (usually a radial, 2 cubital cells and a discoidal cell; Southern and Southwestern) .....  
     .....PSEUDOMYRMINAE Emery (one genus, *Pseudomyrma* Guérin, p. 291
- Clypeus extending back between frontal carinae (fig. 1, C); eyes not as described above; not especially elongate, slender ants; antenna 10- to 13-segmented; Mayrian furrows present or absent. MYRMICINAE Lepeletier, p. 291
3. (1) A pronounced constriction between the first and second gastric segments (fig. 3, A) ..... 4
- No pronounced constriction between the first and second gastric segments\* (fig. 3, C) ..... 5
4. (3) Hypopygium strongly forked (fig. 6, C); no cerci; genital appendages entirely retractile; mandibles well developed; (rare; Texas and Arizona) ..... CERAPACHYINAE Forel, p. 288

\* The male of *Eciton (Labidus) esenbecki* (Westwood) has a pronounced constriction between the first and second gastric segments.

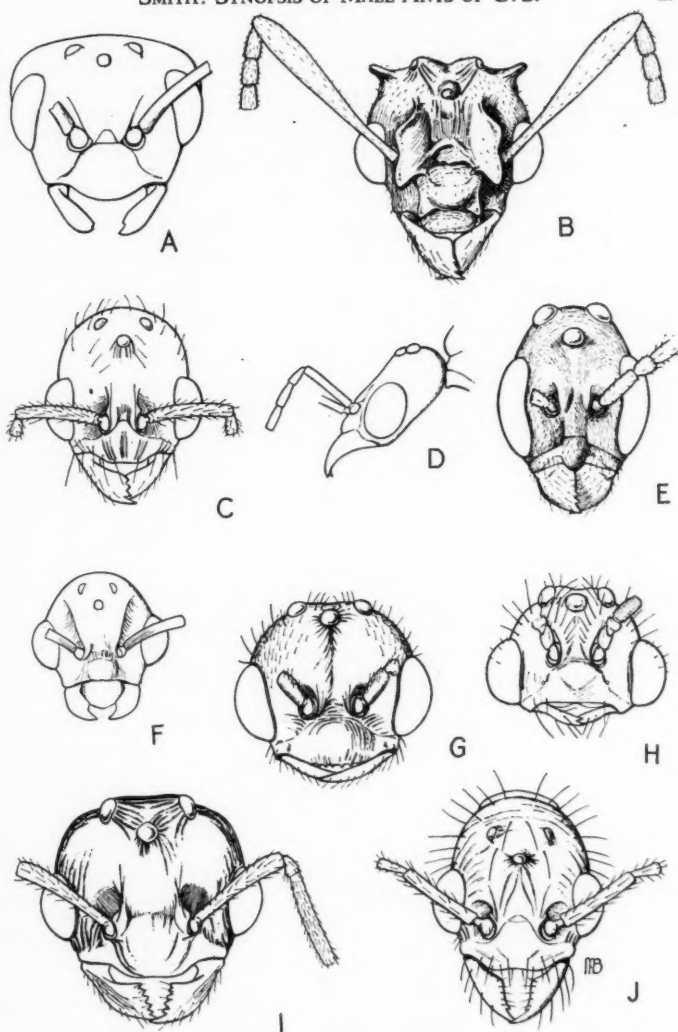


Fig. 1.—Head: A, *Formica truncicola integra* Nylander; B, *Cyphomyrmex* sp.; C, *Stenamma* sp.; D, *Aphaenogaster fulva aquia* (Buckley); E, *Pseudomyrma brunnea* F. Smith; F, *Harpagoxenus americanus* (Emery); G, *Stigmatomma pallipes* (Haldeman); H, *Solenopsis geminata rufa* (Jerdon); I, *Tetramorium caespitum* (Linnaeus); J, *Novomessor cockerelli* André.

- Hypopygium entire or at most not strongly forked; cerci present but not always clearly visible; genital appendages usually nonretractile; mandible often poorly developed ..... Ponerinae Lepeletier, p. 278
5. (3) Hypopygium with 2 or 3 apical teeth (fig. 4, *E*); (genital appendages entirely retractile); frontal carinae not covering antennal insertions; antenna 13-segmented; eyes and ocelli well developed; a radial, 2 cubital, and 2 discoidal cells (fig. 5, *A*); large, wasplike ants; (mainly Southern and Southwestern) ..... Dorylinae Leach (one genus *Eciton* Latreille), p. 290
- Hypopygium not as described above; frontal carinae usually covering the antennal insertions; not unusually large, wasplike ants ..... Dolichoderinae Forel, p. 309, and Formicinae Lepeletier, p. 309

### Subfamily Ponerinae Lepeletier

1. Wingless; ergatandrous; (rare) ..... *Ponera* Latreille (part), p. 286
1. Winged; normal ..... 2
2. (1) Tarsal claws comblike (fig. 2, *K*); antenna very long subfiliform (fig. 2, *A*); Mayrian furrows present; no spine on pygidium; (Florida, Georgia, and Texas) ..... *Lepogenys*, subgenus *Lobopella* Mayr, p. 286
- Tarsal claws simple (fig. 2, *M*) or toothed (fig. 2, *L*), never comblike ..... 3
3. (2) No discoidal or radial cells, but a large cubital cell; (Mayrian furrows absent; metanotum with a distinct spine (fig. 3, *D*); petiole scalelike); probably confined to the eastern half of the United States; (uncommon) ..... *Proceratium* Roger, p. 282
- One or 2 discoidal cells, 2 cubital cells, or else 1 cubital cell and an indication of another cell, and a radial cell ..... 4
4. (3) Tarsal claws weakly to strongly toothed (the teeth sometimes very indistinct) 5
- Tarsal claws simple (fig. 2, *M*) ..... 9
5. (4) Mayrian furrows distinct (fig. 3, *F*) ..... 6
- Mayrian furrows absent or obsolescent ..... 8
6. (5) Mandible large (subtriangular), toothed (fig. 2, *F*); tarsal claws distinctly toothed; pygidium spineless; (Texas) ..... *Ectatomma*, subgenus *Ectatomma* F. Smith, p. 280
- Mandible usually small, toothless ..... 7
7. (6) Length 8 mm.; sculpture on epinotum forming somewhat of an inverted V; (petiolar node higher than long; pygidium spined (fig. 3, *A*)); Texas and Louisiana ..... *Pachycondyla*, subgenus *Pachycondyla* F. Smith, p. 282
- Length 12 mm.; sculpture on epinotum not forming an inverted V; Texas ..... *Neoponera*, subgenus *Neoponera* Emery, p. 284
8. (5) Petiolar node bluntly pointed above, not forming a spine; mandible extremely small; (antenna subfiliform; eyes subreniform; pygidium spined); Florida, Georgia, Texas, Louisiana, and Arizona ..... *Odontomachus* Latreille, p. 286
- Petiolar node not as described above, the posterior border bisinuate, forming 3 toothlike projections; mandible large (subtriangular); body covered with coarse pitlike punctures; (uncommon); Texas ..... *Platythyrea* Roger, p. 280
9. (4) Anterior border of clypeus with small but distinct denticulae (fig. 1, *G*); mandible long and narrow, tapering apically to a sharp point (fig. 2, *J*); (Mayrian furrows present; petiole of somewhat similar conformation to that of worker; entire United States) ..... *Stigmatomma* Roger, p. 280
- Anterior border of clypeus not as described above; mandible of a different shape ..... 10

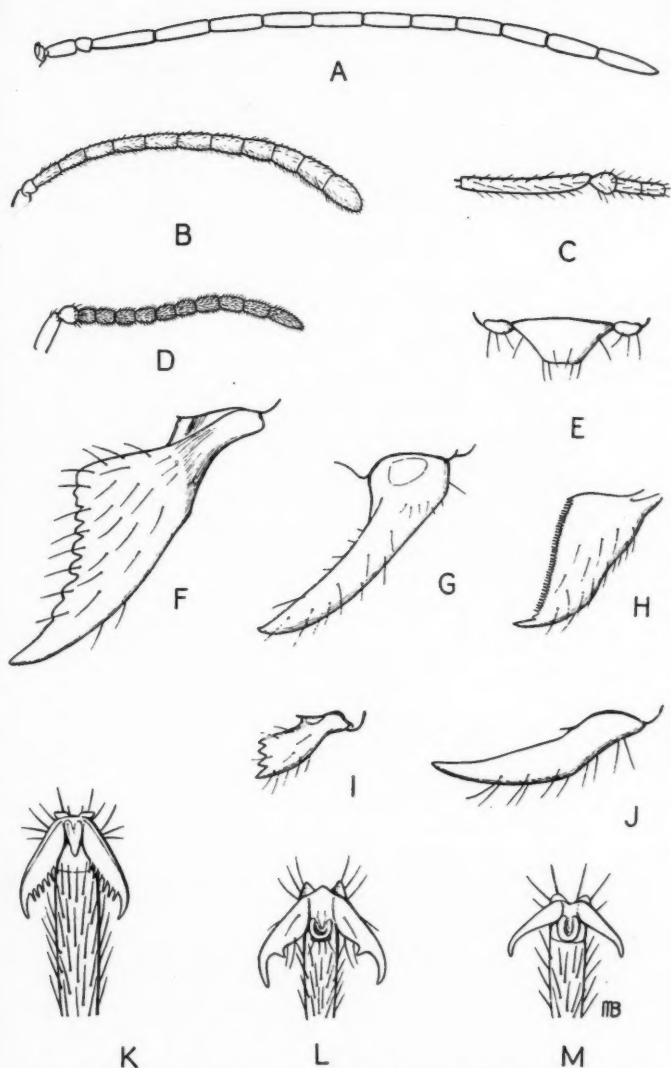


Fig. 2.—Antenna: A, *Leptogenys* (*Lobopelta*) *elongata* (Buckley); B, *Cryptocerus* sp.; C, *Lasius* sp.; D, *Crematogaster atkinsoni* Wheeler. Mandible: E, *Myrmecina graminicola americana* Emery; F, *Atta texana* Buckley; G, *Polyergus lucidus* Mayr; H, *Tapinoma sessile* (Say); I, *Monomorium minimum* (Buckley); J, *Stigmatomma pallipes* (Haldeman); Tarsal claw: K, *Leptogenys* (*Lobopelta*) *elongata* (Buckley); L, *Eciton* (*Labidus*) *coecum* (Latreille); M, *Sysphincta pergandei* Emery.

10. (9) Metanotum extended posteriorly as a prominent spine or tubercle (fig. 3, D); (rare; eastern half of United States).....*Sysphincta* Roger, p. 284  
 Metanotum not extended posteriorly as a prominent spine or tubercle .....11
11. (10) Hind tibia with a single spur; entire United States, more common in the southern half .....*Ponera* Latreille (part), p. 286  
 Hind tibia with 2 spurs (fig. 4, G), the smaller of these sometimes very difficult to see; Gulf and Southeastern States .....*Euponera*, subgenera *Brachyponera* Emery, p. 282, and *Trachymesopus* Emery, p. 284

#### STIGMATOMMA Roger

*Stigmatomma* Roger, 1859, Berlin Ent. Ztschr. 3:250.

Genotype, *Stigmatomma denticulatum* Roger (by designation of Bingham, 1903).

Length 3-4.5 mm. Antenna 13-segmented; scape short, approximating length of second funicular segment; all funicular segments except the first distinctly longer than broad. Mandible elongate, slender, ending in a sharp, apical point (Fig. 2, J). Anterior border of clypeus minutely denticulate (Fig. 1, G.) Antennal fossa almost touching posterior border of clypeus. Eye placed close to base of mandible. Thorax with Mayrian furrows and parapsidal sutures. Wing with prominent stigma; a radial, 2 cubital, and 2 discoidal cells. Petiole of a conformation somewhat similar to that of worker. Constriction between petiole and first gastric segment very strong, that between first and second gastric segments less pronounced. Posterior surface of thorax with margined, subcircular area. Hind tibia with 2 spurs. Genital appendages not large. Cerci present.

*S. pallipes* (Haldeman) and its 3 subspecies. One or more of these occur in nearly every section of the United States; *pallipes* is the most common in the eastern half of the country. Species examined, *S. pallipes*.

#### PLATYTHYREA Roger

*Platythyrea* Roger, 1863, Berlin Ent. Ztschr. 7: 172.

Genotype, *Pachycondyla punctata* F. Smith (by designation of Bingham, 1903).

Length 7.3 mm. Antenna 13-segmented; scape a little shorter than second funicular segment. Mandible well developed, subtriangular. Eyes and ocelli not large. Pronotum large, not covered by mesonotum. Mayrian furrows present. Wing with 2 cubital cells. Petiole similar to that of worker. Hind tibia with 2 spurs. Pygidium rounded. Cerci present. Body covered with a pruinose pubescence.

One species, *punctata* (F. Smith) of extreme southern Texas. Uncommon. I have not been able to examine any males of this genus. The description above is adapted from Emery, 1911, in Wytsman's *Genera Insectorum* (fasc. 118: 28). The measurement is that of F. Smith, 1858 (Cat. Hymen. Brit. Mus. 6: 108).

#### ECTATOMMA, subgenus ECTATOMMA F. Smith

*Ectatomma* F. Smith, 1858, Catalogue of Hymenopterous Insects in the Collection of the British Museum, pt. 6, p. 102.

Subgenotype, *Formica tuberculata* Olivier (by designation of Bingham, 1903).



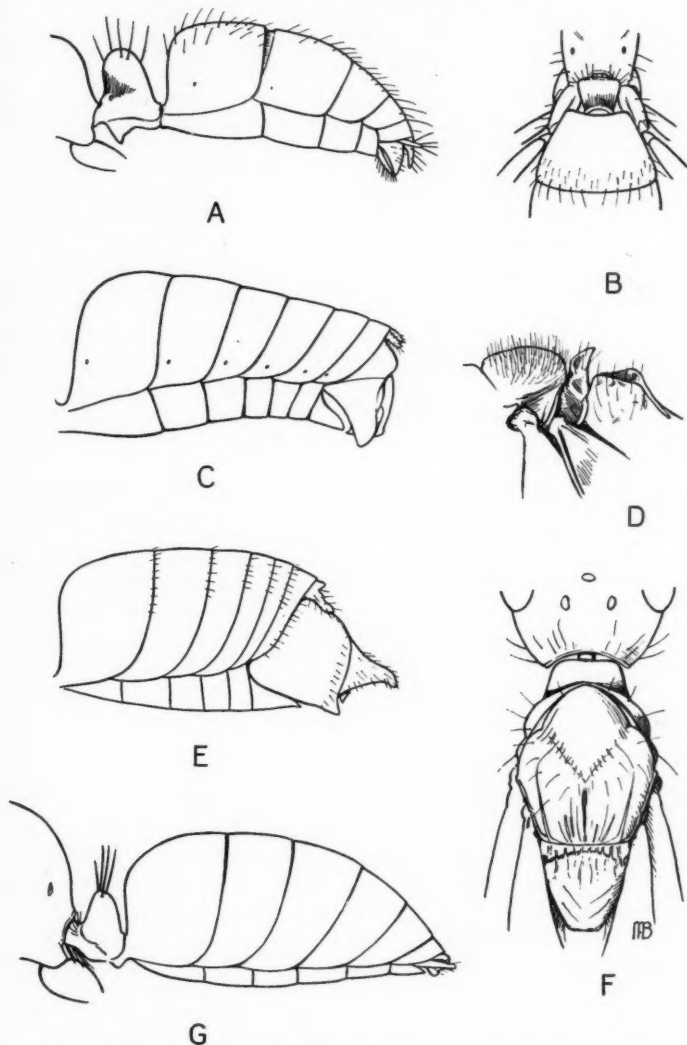


Fig. 3.—Petiole and gaster: A, *Pachycondyla harpax* (Fabricius); B, *Prenolepis imparis* (Say); G, *Camponotus castaneus* (Fabricius). Gaster: C, *Formica truncicola* Nylander; E, *Liometopum apiculatum luutosum* Wheeler. Thorax: D, *Proceratium croceum* Roger; F, *Myrmica punctiventris* Roger.

Length 10-11 mm. Antenna 13-segmented, unusually long; scape extremely short; funiculus subfiliform, with first segment distinctly broader than long. Mandible large, subtriangular, toothed. Mayrian furrows distinct. Wing with a radial, 2 cubital, and 2 discoidal cells. Tarsal claws clearly toothed. A strong constriction between petiole and first gastric segment, and also between first and second gastric segments. Pygidium without a spine. Cerci present.

Only one species, the introduced *tuberculatum* (Olivier), of Texas. Species examined, *tuberculatum*.

#### ECTATOMMA, subgenus PARECTATOMMA Emery

*Ectatomma* (*Parectatomma*) Emery, 1911, Wytman's Gen. Insect., Fasc. 118:44. Subgenotype, *Ectatomma* (*Gnamptogenys*) *triangulare* Mayr (by original designation).

This subgenus is represented by only one species, the native *hartmanni* Wheeler of Texas, the male of which is unknown.

#### PROCERATIUM Roger

*Proceratium* Roger, 1863, Berlin Ent. Ztschr. 7: 171. Genotype, *Proceratium silaceum* Roger (monobasic).

Length 3.4-2.5 mm. Antenna 13-segmented. Frontal carinae not covering antennal insertions. Mandible large, subtriangular. Thorax without Mayrian furrows but with parapsidal sutures. Metanotum spined (Fig. 3, D). Wing without radial or discoidal cell but with a very large cubital cell. Tarsal claws simple (Fig. 2, M). Petiole, in profile, scalelike, very much smaller than first gastric segment. A very pronounced constriction between first and second gastric segments. Pygidium without a spine. Cerci present.

Three species, 1 subspecies, and a variety which are confined to the southeastern fourth of the United States. Uncommon. Species examined, *croceum* (Roger), *silaceum* Roger, and *crassicornis* Emery.

#### PACHYCONDYLA, subgenus PACHYCONDYLA F. Smith

*Pachycondyla* F. Smith, 1858, Catalogue of Hymenopterous Insects in the Collection of the British Museum, pt. 6, p. 105. Subgenotype, *Formica crassinoda* Latreille (by designation of Emery, 1901).

Differing from *Neoponera*, subgenus *Neoponera*, as follows: Smaller (8 mm.); mandible sometimes less elongate; sculpture on epinotum somewhat in the shape of an inverted V; constriction between first and second gastric segments distinct but not so pronounced.

One species, *harpax* (Fabricius) of Texas and Louisiana. Species examined, *harpax*.

#### EUPONERA, subgenus BRACHYPONERA Emery

*Euponera* (*Brachyponera*) Emery, 1901, Soc. Ent. de Belg. Ann. 45:43. Subgenotype, *Ponera sennaarensis* Mayr (by original designation).

Length 3-4 mm. Characters same as for *Ponera* except for the following: Middle and hind tibiae each with 2 spurs (Fig. 4, G), one of which is small

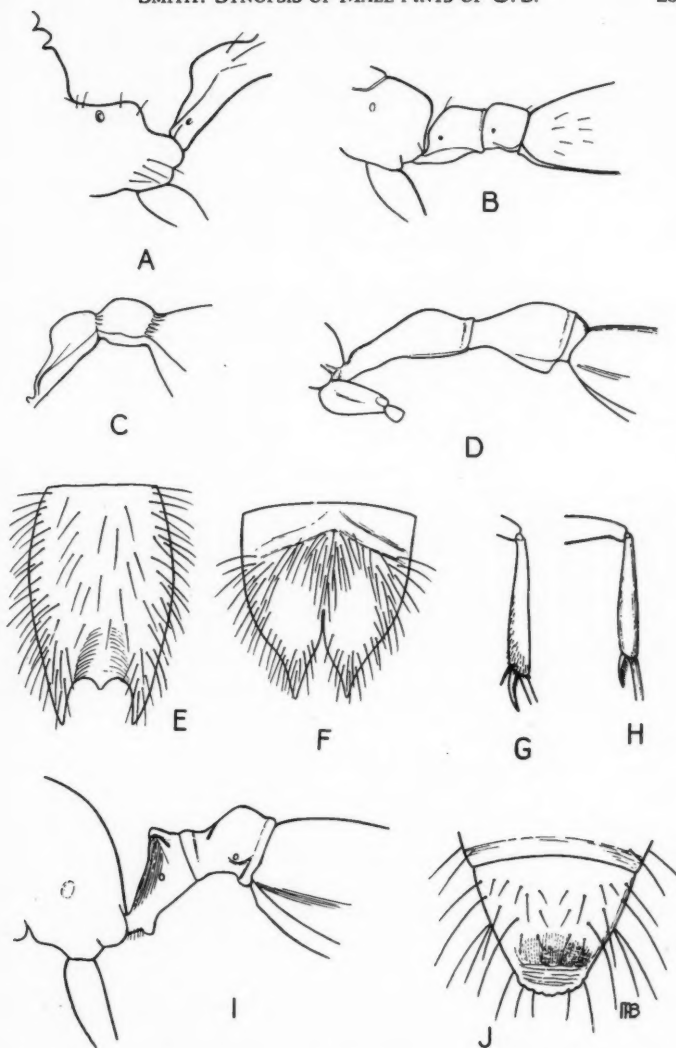


Fig. 4.—Posterior part of thorax: A, *Stenamma brevicorne* (Mayr). Petiole and postpetiole: B, *Xenomyrmex stollii floridanus* Emery; C, *Stenamma* sp.; D, *Pseudomyrma brunnea* F. Smith; I, *Solenopsis geminata rufa* (Jerdon). Hypopygium: F, *Eciton (Labidus) coecum* (Latreille); E, *Eciton (Neivamyrmex) harrisi* (Haldeman). Pygidium: J, *Acanthostichus (Ctenopyga) townsendi* Ashmead. Hind tibia: G, *Euponera (Trachymesopus) gilva* (Roger); H, *Myrmica punctiventris* Roger.

and difficult to see; Mayrian furrows present or absent, and spine present or lacking on pygidium.

A single, introduced species, *solitaria* (F. Smith), which is present in several towns in Georgia, North Carolina, and Virginia, especially the coastal towns. Species examined, *solitaria*.

#### EUPONERA, subgenus TRACHYMESOPUS Emery

*Euponera* (*Trachymesopus*) Emery, 1911, Wytzman's Genera Insect., Fasc. 118, p. 84. Type of subgenus, *Formica stigma* Fabricius (by original designation).

Characters similar to those of *Euponera*, subgenus *Brachyponera*.

Two species, *stigma* (Fabricius) of Florida and *gilva* (Roger) of Alabama, Mississippi, Tennessee, and Texas. Species examined, *stigma* and *gilva*.

#### SYSPHINCTA Roger

*Sysphincta* Roger, 1863, Berlin. Ent. Ztschr. 7: 175.

Genotype, *Sysphincta micrommata* Roger (monobasic).

Length 3-4mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 3 funicular segments. Mandible well developed, subtriangular, with a long apical tooth. Frontal carinae very close to each other basally, not covering antennal insertions. Posterior border of head well rounded. Ocelli prominent, not on a protuberance at vertex of head. Eye moderately convex, not touching base of mandible. Parapsidal sutures but no Mayrian furrows. Metanotum with a prominent spine or tubercle (Fig. 3, *D*). Wing with a prominent stigma, a radial and a discoidal cell, and a large cubital cell which is partly divided by a longitudinal vein; brownish. Tarsal claws simple (Fig. 2, *M*). Petiole nodiform. An unusually strong constriction between first and second gastric segments. Pygidium without a spine. Genital appendages not prominent.

Rare. *Sysphincta pergandei* Emery, which occurs throughout the eastern half of the United States, is the only species. Species examined, *pergandei*.

#### NEOPONERA, subgenus NEOPONERA Emery

*Neoponera* Emery, 1901, Soc. Ent. de Belg. Ann. 45: 40.

Subgenotype, *Formica villosa* Fabricius (by original designation).

Length 12 mm. Antenna 13-segmented, unusually long; scape exceedingly short but distinctly longer than first funicular segment. Mandible vestigial, very short, but longer than broad. Thorax with Mayrian furrows and parapsidal sutures (Fig. 3, *F*). Wing with a radial, 2 cubital, and 2 discoidal cells. Tarsal claws toothed (Fig. 2, *L*). Sculpture on epinotum not forming an inverted V. Middle and hind tibiae each with 2 spurs (Fig. 4, *G*). Petiole robust, higher than long, separated from first gastric segment by an unusually strong constriction. Pygidium with a spine (Fig. 3, *A*). Cerci present.

One species, *villosa* (Fabricius) of Texas. Species examined, *villosa*.

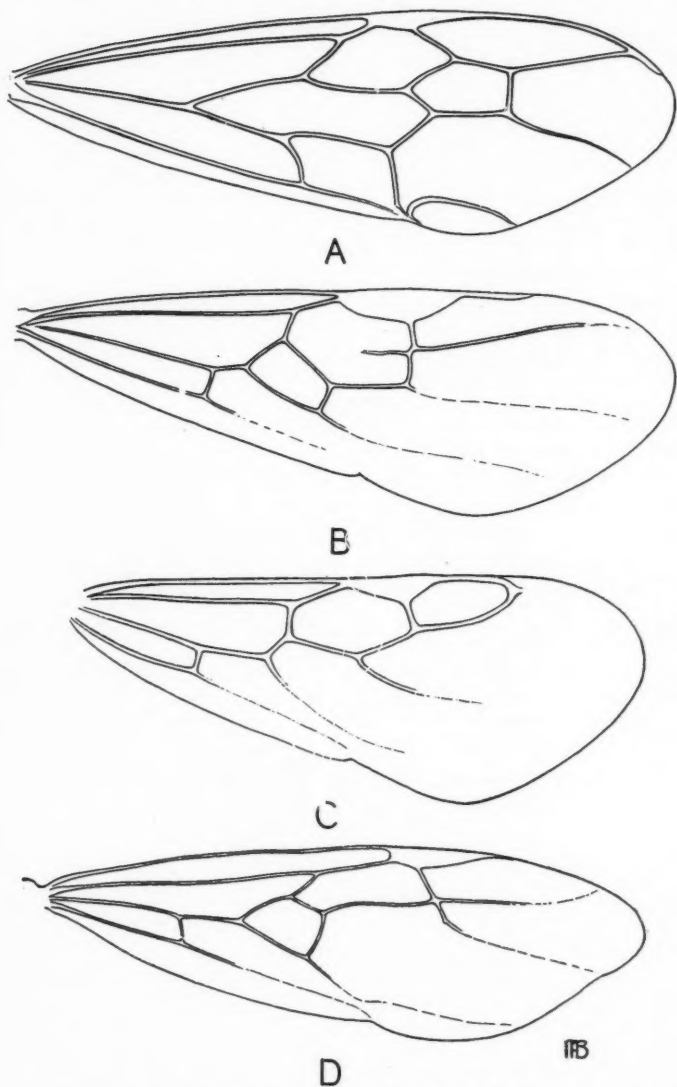


Fig. 5.—Wing: A, *Eciton (Labidus) coecum* (Latreille); B, *Myrmica punctiventris* Roger; C, *Myrmecina graminicola americana* Emery; D, *Veromessor pergandei* (Mayr).

## PONERA Latreille

*Ponera* Latreille, 1802, Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes, vol. 4, p. 128.

Genotype, *Formica coarctata* Latreille (monobasic).

Length 3-3.5 mm. Antenna 13-segmented; scape usually shorter than second funicular segment. Mandible vestigial. Eye placed close to base of mandible. Parapsidal sutures but no Mayrian furrows. Wing with a radial, 2 cubital, and a discoidal cell. Middle and hind tibiae each with a single spur. Constriction between first and second gastric segments pronounced. Pygidium with a spine (Fig. 3, A). Cerci present.

Entire United States. Four species, 1 subspecies, and a variety. *P. coarctata pennsylvanica* (Buckley) is the most common form in the eastern half of the United States. Ergatandrous males occur in at least 3 species, *ergatandria* Forel, *opaciceps* Mayr, and *oblongiceps* M. R. Smith. These workerlike males are characterized by their 12- (*ergatandria*) or 13-segmented (*opaciceps*, *oblongiceps*) antennae; wingless, workerlike thorax, and gaster bearing male genitalia. Species examined, *coarctata pennsylvanica*, *trigona* var. *opacior* Forel, and the ergatandrous males of *opaciceps* and *oblongiceps*.

## LEPTOGENYS, subgenus LOBOPELTA Mayr

*Lobopelta* Mayr, 1862, Zool.-Bot. Gesell. Wien, Verh. 12:733.

Subgenotype, *Ponera diminuta* F. Smith (by designation of Bingham, 1903).

Length 5-6 mm. Antenna 13-segmented; funiculus very long, subfiliform (Fig. 2, A). Mandible vestigial, consisting of a narrow, edentate stub. Eye large, subreniform. Thorax with distinct Mayrian furrows; parapsidal sutures weakly developed or absent. Wing with a radial, 2 cubital, and 2 discoidal cells. Tarsal claws distinctly comblike (Fig. 2, K). Cerci present. Pygidium without a spine. Stipes rather large.

One species, *elongata* (Buckley) of Florida, Georgia, and Texas, and its subspecies *manni* Wheeler of Florida. Species examined, *elongata*.

## ODONTOMACHUS Latreille

*Odontomachus* Latreille, 1802, Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes, vol. 4, p. 128.

Genotype, *Formica haematoda* Linnaeus (monobasic).

Length 6.5-8 mm. Antenna 13-segmented, unusually long; scape extremely short; funiculus subfiliform. Mandible vestigial, very short, stubby and edentate. Eye large, subreniform. Parapsidal sutures present but no Mayrian furrows. Wing with a radial, 2 cubital, and 2 discoidal cells. Tarsal claws weakly toothed. Summit of petiole bluntly pointed but not forming a distinct spine; ventral border with a pronounced tooth. Pygidium with a spine (Fig. 3, A). Cerci present. Genitalia large.



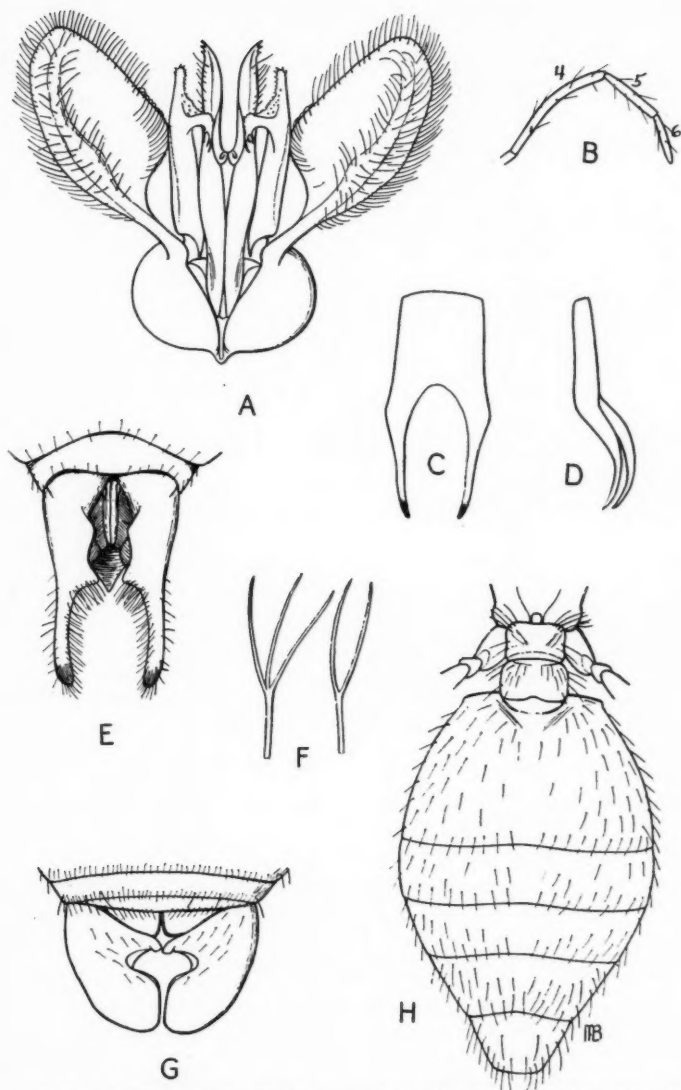


Fig. 6.—Maxillary palpus: B, *Myrmecocystus* sp. Genitalia: A, *Eciton* (*Labidus*) *coecum* (Latreille); C, *Wasmannia auropunctata* (Roger); D, *Acromyrmex* (*Moellerius*) *versicolor* (Pergande). Hypopygium: E, *Cerapachys* (*Parasyscia*) *augustae* Wheeler. Hairs: F, *Triglyphothrix striatidens* (Emery). Petiole, postpetiole, and gaster: G, *Crematogaster* (*Acrocoelia*) *atkinsoni* Wheeler.

Four subspecies of *haematoda* (Linnaeus), *insularis* Guérin of Florida and Georgia, *coninodis* Wheeler of Arizona, *desertorum* Wheeler of Arizona, and *clarus* Roger of Texas and Louisiana. The description above is based on males of *insularis*.

#### Subfamily CERAPACHYINAE Forel

1. Mayrian furrows absent; wing venation highly variable, often with only vestiges of cells but usually with a discoidal cell and sometimes a cubital cell; pygidium without an impressed or flattened area; hypopygium with a slender, forked process (fig. 6, *D*); rare; Texas and Arizona .....  
*Cerapachys*, subgenus *Parasyscia* Emery, p. 288
- Mayrian furrows present; wing venation variable, usually 2 to 3 cubital and discoidal cells; pygidium with an impressed or flattened area, the border of which is scalloped (fig. 4, *f*); hypopygium with a stout, forked process; rare; Texas .....  
*Cerapachys*, subgenus *Parasyscia* Emery, p. 288

#### CERAPACHYS, subgenus PARASYSCIA Emery

*Parasyscia* Emery, 1882, André's Species des Hyménoptères d'Europe et d'Algerie, p. 235.

Subgenotype, *Parasyscia piochardi* Emery (monobasic).

Length 3.2-3.7 mm. Similar to *Acanthostichus* (*Ctenopyga*) except for the following: Funiculus not so strongly clavate; frontal carinae not covering antennal insertions; anterior border of clypeus with a distinct, median, toothlike projection; thorax without perceptible Mayrian furrows but with parapsidal sutures; venation highly variable, usually a discoidal cell, and sometimes a cubital cell; pygidium without a flattened or impressed area; hypopygium with a slender, forked process (Fig. 6, *D*).

Rare. Two species, *augustae* Wheeler of Texas and Arizona and *davisi* M. R. Smith of Texas. Males examined of both these species.

#### ACANTHOSTICHUS, subgenus CTENOPYGA Ashmead

*Ctenopyga* Ashmead, 1905, Canad. Ent. 37: 382 (nomen nudum); 1906, Ent. Soc. Wash. Proc. 8: 29.

Subgenotype, *Ctenopyga townsendi* Ashmead (by original designation).

Antenna 13-segmented; funiculus gradually enlarging from base to apex. Mandible large, subtriangular. Frontal carinae partly covering antennal insertions. Thorax with distinct Mayrian furrows and parapsidal sutures. Venation variable; stigma prominent, usually a partly closed radial cell, 2 to 3 cubital and discoidal cells, with one of the discoidal cells often partly closed. First gastric segment, in profile, subcylindrical, very much larger than petiole; a strong constriction between petiole and first gastric segment and also between first and second gastric segments. Gaster, from above, elongate, subelliptical, with pronounced constrictions between segments. Pygidium with an impressed or flattened area, which is strongly sculptured, and the border scalloped (Fig. 4, *f*); hypopygium with a stout, forked process, each fork subtriangular. No cerci.

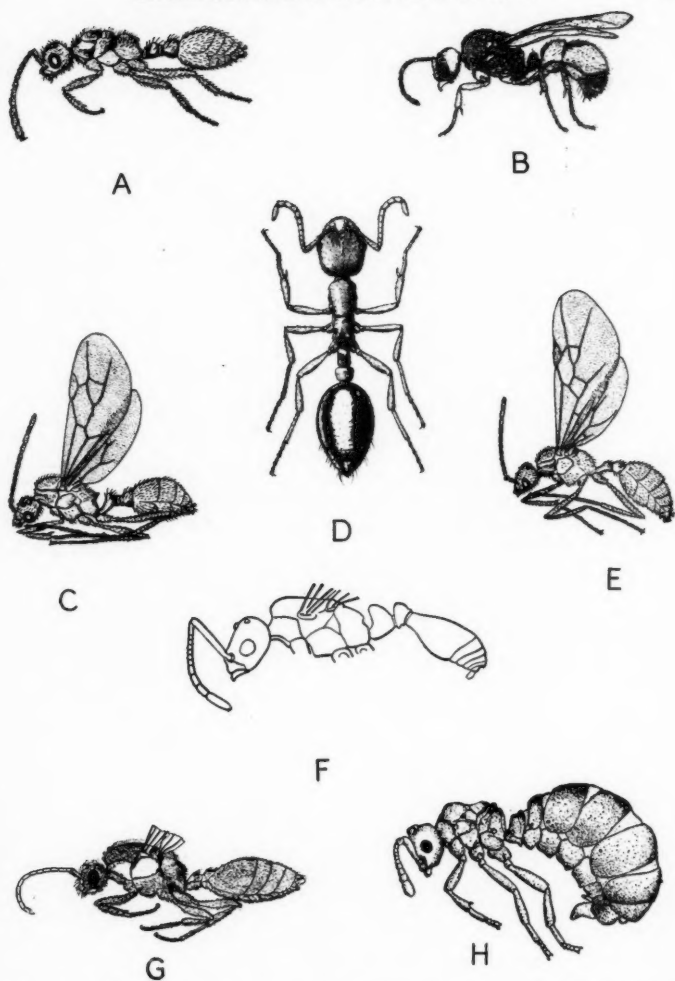


Fig. 7.—Lateral view: A, *Symmyrmica chamberlini* Wheeler (1904, Bull. Amer. Mus. Nat. Hist. 20, pl. 1, fig. 1); B, *Proceratium croceum* (Roger); C, *Epipheidole inquilina* Wheeler (1904, Bull. Amer. Mus. Nat. Hist. 20, pl. 3, fig. 15); E, *Symphedole elecebra* Wheeler (1904, Bull. Amer. Mus. Nat. Hist. 20, pl. 3, fig. 9); F, *Epeocus pergandei* Emery (Ants, W. M. Wheeler, 1926, Columbia University Press, p. 498, fig. 278 a); G, *Erebomyrma longi* Wheeler (1903, Biol. Bull. 4: 144, fig. 5); H, *Anergates atratulus* (Schenck) (Ants, W. M. Wheeler, 1926, Columbia University Press, p. 499, fig. 279 d). Dorsal view: D, *Leptothorax diversipilosus* M. R. Smith.

Rare. One species, *texanus* Forel of Texas, the male of which is unknown. The above description is drawn from that of *townsendi* Ashmead, a Mexican species, the male of which measures approximately 4 mm.

#### Subfamily DORYLINAE Leach

1. Hypopygium with 2 apical teeth (fig. 4, *F*); stipes large, broad, and thin (lamelliform), with ciliated margins (fig. 6, *A*); tarsal claws distinctly toothed; mainly Southwestern.....*Eciton*, subgenus *Labidus* Jurine, p. 290
- Hypopygium with 3 apical teeth (fig. 4, *E*); stipes seldom lamelliform; tarsal claws not toothed or weakly so; Southern and Southwestern .....*Eciton*, subgenus *Neivamyrmex* Borgmeier, p. 290

#### ECITON, subgenus LABIDUS Jurine

*Labidus* Jurine, 1807, Nouvelle Méthode de Classer les Hyménoptères et les Diptères, p. 282.

Subgenotype, (*Labidus latreillei* Jurine)=*Formica coeca* Latreille (by designation of Latreille, 1810).

Length 15-17 mm. Antenna 13-segmented. Mandible large, edentate. Frontal carinae not covering antennal insertions. A radial, 2 cubital, and 2 discoidal cells; first discoidal cell at least 3 times as long as broad (Fig. 5, *A*). Tarsal claws toothed (Fig. 2, *L*). Hypopygium with 2 teeth (Fig. 4, *F*). Stipes large, broad, thin (lamelliform), with ciliated margins (Fig. 6, *A*).

Two species, *coecum* (Latreille) and *esenbecki* (Westwood). The former occurs in Texas, Oklahoma, and Louisiana; the latter in southern Texas. *Eciton esenbecki* is very probably the male of *crassicornis* (F. Smith); if this should prove to be the case, then the name *crassicornis* will have to be synonymized. Species examined, *coecum* and *esenbecki*.

#### ECITON, subgenus NEIVAMYRMEX Borgmeier

*Eciton (Acamatus)* Emery, 1894, Soc. Ent. Ital. Bol. 26: 181 (preoccupied by Schoenherr, 1833).

*Neivamyrmex* Borgmeier, 1940, Rev. de Ent. 11: 606.

Subgenotype, (*Eciton (Acamatus) schmitti* Emery)=*Labidus nigrescens* Cresson (by designation of Wheeler, 1911).

Length 7-13 mm. Characters similar to those of *Eciton (Labidus)* except for the following: Tarsal claws not toothed or weakly so; hypopygium with 3 teeth (Fig. 4, *E*); stipes not large, seldom lamelliform.

Seventeen species. Southern half of United States with a slight northward extension in the Mississippi Valley. Species examined, *arizonense* Wheeler, *carolinense* Emery, *fuscipennis* Wheeler, *harrisii* (Haldeman), *melsheimeri* (Haldeman), *minus* (Cresson), *nigrescens* (Cresson), *opacithorax* Emery, *oslari* Wheeler, *pilosum* F. Smith, and *pilosum mandibulare* M. R. Smith.

## Subfamily PSEUDOMYRMINAE Emery

## PSEUDOMYRMA Guérin

*Pseudomyrma* Guérin, 1844, in Cuvier, Iconographie du règne animal, Insecte, 1844, p. 427.

Genotype, *Formica gracilis* Fabricius (by original designation).

Length 3.5-8 mm. Antenna 12-segmented; scape short, less than combined lengths of first 2 funicular segments; funiculus subfiliform, all segments except the first very much longer than broad. Antennal fossa remote from posterior border of clypeus (Fig. 1, *E*). Median area of anterior border of clypeus rounded or angular. Mandible well developed, subtriangular, with small but well-defined teeth. Eyes large, subreniform. Pronotum often unusually long. Parapsidal sutures present but no Mayrian furrows. Wing with prominent stigma; a radial, 1 or 2 cubital cells, and a discoidal cell. Petiole slender, broadest posteriorly. Gaster elongate. Cerci present. Stipes robust.

Four species and 1 subspecies; one or more of these occur throughout the region from at least South Carolina to California; *gracilis mexicana* Roger extends into Texas from Mexico. Species examined, *gracilis mexicana*, *brunnea* F. Smith, and *flavidula* F. Smith.

## Subfamily MYRMICINAE Lepeletier

1. Antenna with 10 segments; (second funicular segment unusually long, approximating the length of the scape (fig. 1, *I*)) ..... 2
- Antenna with more than 10 segments ..... 4
2. (1) At least some of the hairs trid or branched (fig. 6, *F*); (introduced species, present in a few towns or cities in several of the Southern States) ..... *Triglyphothrix* Forel, p. 305
- Hairs unbranched ..... 3
3. (2) Native species, known only from the warm, dry, open regions of Texas and Arizona ..... *Xiphomyrmex* Forel, p. 305
- Introduced species, usually found in towns or cities. *Tetramorium* Mayr, p. 305
4. (1) Antenna with 11 segments ..... 5
- Antenna with more than 11 segments ..... 9
5. (4) Winged; normal ..... 6
- Wingless; ergatandrous or pupoid ..... 7
6. (5) Gaster from above subcordate, not impressed at base; postpetiole attached to dorsal surface of base of gaster (fig. 6, *H*); scape not so long as the combined lengths of the first 7 or 8 funicular segments ..... *Crematogaster*, subgenus *Orthocrema* Santschi, p. 299
- Gaster from above not subcordate, impressed at base; postpetiole not attached to dorsal surface of base of gaster; scape unusually long, approximating the combined lengths of the first 7 or 8 funicular segments (fig. 7, *F*); (probably a parasitic species in colonies of *Monomorium minimum* (Buckley); extremely rare; District of Columbia).... *Epoecus* Emery (part), p. 301
7. (5) Pupoid; (clypeus emarginate; Mayrian furrows absent; gaster and genital

- appendages large (fig. 7, *H*); parasitic in colonies of *Tetramorium caespitum* (Linnaeus); extremely rare; New Jersey, Delaware, and Virginia) ..... *Anergates* Forel, p. 302  
Ergatandrous ..... 8
8. (7) Clypeus bicarinate, anterior border with a median emargination; non-inquinilous; rare; Florida .....  
    *Cardiocondyla* Emery (part) (*wroughtoni* var. *bimaculata* Forel), p. 299  
Clypeus not bicarinate, or with a distinct emargination; inquinilous species in colonies of *Myrmica mutica* Emery; extremely rare; Utah (fig. 7, *A*) ..... *Symmyrmica* Wheeler, p. 304
9. (4) Antenna with 12 segments ..... 10  
    Antenna with 13 segments ..... 17
10. (9) Wingless; ergatandrous ..... 11  
    Winged; normal ..... 12
11. (10) Inquinilous in nests of *Formica obscuripes* Forel and its subspecies *melanotica* Emery (fig. 7, *D*) .....  
    ..... *Leptothorax*, subgenus *Mychothorax* Ruzsky (part), p. 304  
Noninquinilous; (rare; Florida) .....  
    ..... *Cardiocondyla* Emery (part) (*nuda* var. *minutior* Forel), p. 299
12. (10) Postpetiole attached to dorsal surface of base of gaster; gaster from above subcordate (fig. 6, *H*); (scape very short; funicular segments usually with a somewhat beadlike appearance (fig. 2, *D*); no Mayrian furrows) ..... *Crematogaster*, subgenus *Acrocoelia* Mayr, p. 300  
Postpetiole not attached to dorsal surface of base of gaster; gaster from above not subcordate ..... 13
13. (12) Base of gaster with a prominent impression above; (scape unusually long, approximately as long as the combined lengths of the first 7 or 8 funicular segments; Mayrian furrows absent (fig. 7, *F*); extremely rare; probably parasitic in colonies of *Monomorium minimum* (Buckley); District of Columbia) ..... *Epoecus* Emery (part), p. 301  
Base of gaster not impressed above ..... 14
14. (13) Petiole non pedunculate (fig. 4, *B*); (scape approximately as long as the combined lengths of the first 2 funicular segments; Mayrian furrows distinct; venation of wings greatly reduced; no radial, cubital, or discoidal cells; rare; approximately 2 mm. in length; Florida) .....  
    ..... *Xenomyrmex* Forel, p. 301  
Petiole more or less pedunculate ..... 15
15. (14) First funicular segment annular or globular (fig. 1, *H*); no Mayrian furrows; (scape very short; ocelli on high summitlike protuberance at vertex of head) ..... *Solenopsis* Westwood, p. 301  
First funicular segment not annular or globular but sometimes noticeably wide; Mayrian furrows present but sometimes weakly indicated ..... 16
16. (15) Antennal scrobe weakly to moderately well developed (fig. 1, *F*); slave-making forms on several species of *Leptothorax*; (Virginia and Ohio northward into Canada; uncommon) ..... *Harpagoxenus* Forel, p. 304  
Antennal scrobe absent; mostly independent or free living forms; (the inquinilous species occur mostly, if not altogether, in the subgenus *Mychothorax* Ruzsky ..... *Leptothorax*, subgenera *Leptothorax* Mayr (part), p. 303, and *Mychothorax* Ruzsky (part) p. 304
17. (9) Scape very long, approximately as long as, or longer than, the combined lengths of the first 8 funicular segments ..... 18  
Scape shorter ..... 23



18. (17) Veins well developed, a radial and a cubital cell but no discoidal cell .....19  
 Veins almost obsolete, no radial, cubital, or discoidal cells; (uncommon);  
*Macromischa* Roger, p. 303
19. (18) Radial cell very narrow, at least 6 times as long as broad; Mayrian  
 furrows absent or obsolescent; length 12 mm. or more; (Texas and  
 Louisiana) .....*Atta* Fabricius, p. 308  
 Radial cell at most approximately 3 times as long as broad; Mayrian  
 furrows present; length less than 12 mm. ....20
20. (19) Length 8 mm.; (stipes large and stout, inwardly curved, with inner basal  
 tooth and truncate apex (fig. 6, G); dorsal surface of first gastric  
 segment with a lateral impression near the base and a median impression  
 more posteriorly; Arizona and Texas) .....*Acromyrmex*, subgenus *Moellerius* Forel, p. 308  
 Length less than 8 mm. ....21
21. (20) Antennal club 4-segmented; length of body approximately 3-5 mm.;  
 (hairs hooked or curved) .....*Trachymyrmex* Forel, p. 307  
 No antennal club; length usually less than 3 mm.; (frontal carinae  
 unusually large, greatly elevated (fig. 1, B)) .....22
22. (21) Hairs of body not hooked or curved; Florida, Texas, Arizona, and  
 California .....*Cyphomyrmex*, subgenus *Cyphomyrmex* Mayr, p. 307  
 Hairs of body hooked or curved; Texas .....*Cyphomyrmex*, subgenus *Mycetosoritis* Wheeler, p. 307
23. (17) Radial cell short, appendiculate (fig. 5, C). the appendix sometimes  
 vestigial .....24  
 Radial cell either absent or else not as described above (if appendiculate,  
 the cell is long) .....25
24. (23) Mandible well developed, subtriangular, toothed; scape as short as, or  
 shorter than, second funicular segment; discoidal cell present; (funiculus  
 strongly enlarging toward apex, clavate (fig. 2, B); Florida,  
 Arizona, and Texas) .....*Cryptocerus*, subgenus  
*Cryptocerus* Fabricius, p. 306, and *Cyathomyrmex* Creighton, p. 306  
 Mandible vestigial, represented by a short, blunt, toothless stub (fig. 2,  
 E); scape longer than second funicular segment; discoidal cell absent;  
 (labrum usually exposed) .....*Myrmecina* Curtis, p. 302
25. (23) Spurs of middle and hind tibiae distinctly pectinate (fig. 4, H) .....26  
 Spurs of middle and hind tibiae either simple or indistinctly pectinate .....28
26. (25) Mayrian furrows well developed (fig. 3, F); (first and second cubital  
 cells partly separated by a longitudinal vein (fig. 5, B)) .....27  
 Mayrian furrows usually absent or else usually weakly developed; (hairs  
 of body long and sometimes rather dense; western half of United States  
 with the exception of one species, *badius* (Latreille), which ranges along  
 the Coastal States from Louisiana into New Jersey).....*Pogonomyrmex*,  
 subgenera *Pogonomyrmex* Mayr, p. 296, and *Ephebomyrmex* Wheeler, p. 296
27. (26) Antenna with a distinct club of 4 or 5 segments; entire United States....  
*Myrmica*, subgenus *Myrmica* Latreille, p. 295  
 Antenna without a distinct club; Western States .....*Myrmica*, subgenus *Manica* Jurine, p. 295
28. (25) Stigma weakly developed or missing; (sides of head strongly converging  
 anteriorly; scape short, funiculus long and subfiliform; Mayrian furrows  
 present; veins poorly developed, indistinct in apical half of wing;  
 uncommon) .....*Strumigenys*,

- subgenera *Strumigenys* F. Smith, p. 306, and *Trichoscapa* Emery, p. 307  
 Stigma not weakly developed or missing, though sometimes pale .....29
29. (28) Petiole scarcely pedunculate; (scape approximately as long as the combined lengths of the first 2 funicular segments; no definite Mayrian furrows; a radial, a cubital, and a discoidal cell; wings brownish at base and hyaline toward apex (fig. 7, G); rare; north Texas) .....  
*Erebomyrma* Wheeler, p. 302  
 Petiole pedunculate ..... 30
30. (29) Stigma at middle of anterior border of wing; (scape long, at least as long as the combined lengths of the first 5 funicular segments; prothorax with well-defined humeral angles; no Mayrian furrows; usually a cubital but no radial or discoidal cell; length approximately 2 mm.; uncommon; Florida) .....*Cardiocondyla* Emery (part), p. 299  
 Stigma not at middle of anterior border of wing .....31
31. (30) Stipes unusually large, very long and slender, with a prominent inner basal tooth (fig. 6, E); (scape short, approximately as long as the combined lengths of the first 2 funicular segments; funiculus long and slender, with the first segment pyriform; Mayrian furrows present; introduced species; Florida) .....*Wasmannia* Forel, p. 305  
 Stipes not as described above, or, if somewhat similar, the other characters do not agree .....32
32. (31) Head, in profile, unusually flattened (fig. 1, D); (scape approximately as long as the combined lengths of the first 3 funicular segments; 2 cubital and 1 discoidal cell but the radial cell not clearly closed; legs slender; epinotum with a pair of tubercles) .....  
*Aphaenogaster*, subgenus *Attomyrma* Emery, p. 297  
 Head, in profile, not unusually flattened .....33
33. (32) Wing normally with 2 closed cubital cells (*Pheidole*, *Sympheidole*, and *Epipheidole*) .....34  
 Wing normally with 1 closed cubital cell (wing venation in *Stenamma* highly variable, this also sometimes true of *Leptothorax*) .....36
34. (33) Mayrian furrows present but often not very distinct; (first funicular segment noticeably wide, somewhat annular or subglobular; ocelli borne on a high protuberance at summit of head (fig. 1, H)) .....  
*Pheidole*, subgenus *Pheidole* Westwood, p. 298  
 Mayrian furrows absent .....35
35. (34) Mandible with a single apical tooth; epinotum rounded, unarmed; discoidal cell present (fig. 7, E); parasitic in colonies of *Pheidole ceres* Wheeler; rare; Colorado .....*Sympheidole* Wheeler, p. 299  
 Mandible with 2 or 3 apical teeth; epinotum with 2 prominent spines; no discoidal cell (fig. 7, C); parasitic in colonies of *Pheidole pilifera* (Roger) and its subspecies *coloradensis* Emery; rare; Nebraska and Colorado .....*Epipheidole* Wheeler, p. 299
36. (33) Six mm. or more in length .....37  
 Less than 6 mm. in length .....38
37. (36) Legs unusually long and slender; (head narrow dorsoventrally, flattened beneath, moderately convex above; posterior border of head slightly constricted above to form a weak flange (fig. 1, J); Texas, New Mexico, and Arizona) .....*Novomessor* Emery, p. 297  
 Legs slender but not unusually long; (intercubitus absent due to the fusion of the radial and cubital veins (fig. 5, D); Colorado, Nevada, Arizona, and California) .....*Veromessor* Forel, p. 298

38. (36) Scape very short, approximately as long as the combined lengths of the first 2 funicular segments or less; (no Mayrian furrows; a cubital cell but no radial cell, discoidal cell present or absent) ..... 39  
 Scape usually longer than the combined lengths of the first 2 funicular segments ..... 40
39. (38) Scape approximately as long as the combined lengths of the first 2 funicular segments; (mandible slender, with several teeth (fig. 2, I); ocelli small); no radial or discoidal cells; native and introduced species ..... *Monomorium*, subgenus *Monomorium* Mayr, p. 300  
 Scape much swollen, even shorter than the second funicular segment; (first funicular segment globular; succeeding segments gradually narrowing toward apex of funiculus); discoidal cell usually present but radial cell missing; introduced species, present in a few southern towns or cities ..... *Monomorium*, subgenus *Parholcomyrrex* Emery, p. 300
40. (38) Without a radial cell ..... 41  
 Radial cell present or absent; (Mayrian furrows present but often not clearly defined; antenna usually with a well-differentiated club; discoidal cell present or absent) .....  
 ..... *Leptothorax*, subgenus *Leptothorax* Mayr (part), p. 303
41. (40) Discoidal cell usually present; 1 to 2 cubital cells; Mayrian furrows usually present but sometimes obsolescent or absent; epinotum either somewhat depressed (fig. 4, A) or else angulate; petiole rather strongly pedunculate (fig. 4, C) ..... *Stenamma* Westwood, p. 296  
 Discoidal cell absent; 1 cubital cell; Mayrian furrows absent; (mesonotum strongly convex; wings hyaline, with pale veins and stigma); epinotum not depressed; petiole not so strongly pedunculate .....  
 ..... *Leptothorax*, subgenus *Dichothorax* Emery, p. 303

## Subfamily MYRMICINAE Lepeletier

## MYRMICA, subgenus MYRMICA Latreille

*Myrmica* Latreille, 1802, Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes, vol. 4, p. 141.

Subgenotype, *Formica rubra* Linnaeus (by designation of Girard, 1879).

Length 3.5-6 mm. Antenna 13-segmented; last 4 or 5 funicular segments enlarged into a club. Mandibles well developed, usually subtriangular, toothed. Eye often strongly convex; ocelli small. Thorax with distinct Mayrian furrows (Fig. 3, F). Wing with first and second cubital cells partly separated by a longitudinal vein (Fig. 5, B). Tibial spurs strongly pectinate (Fig. 4, H). Cerci present.

Widely distributed over the United States; 4 species, 7 subspecies, and 20 varieties. Species examined, *brevinodis* Emery and its varieties *canadensis* Wheeler and *sulcinodoides* Emery; *punctiventris* Roger, *rubra laevinodis* Nylander, *scabrinodis sabuleti americana* Weber, *scabrinodis* var. *fracticornis* Emery, and *scabrinodis schenckii* var. *emeryana* Forel.

## MYRMICA, subgenus MANICA Jurine

*Manica* Jurine, 1807, Nouvelle Méthode de Classer les Hyménoptères et les Diptères, p. 276.

Subgenotype, *Formica rubida* Latreille (by designation of Wheeler, 1911).

Characters similar to those of the subgenus *Myrmica* except that the males are generally larger (6.7.5 mm.) and do not have the last 4 or 5 funicular segments enlarged into a club. The subgenus *Manica* contains 5 species which are apparently confined to the Western States. Species examined, *mutica* Emery, the only one in which males are known.

POGONOMYRMEX, subgenus POGONOMYRMEX Mayr

*Pogonomyrmex* Mayr, 1868, Soc. dei Nat. di Modena Ann. 3: 169.

Subgenotype, *Formica badia* Latreille (by designation of Wheeler, 1911).

Length 6.5-11 mm. Antenna 13-segmented; funiculus not forming a club. Eye small, ocelli very much so. Mandible well developed, toothed. Mayrian furrows absent, poorly developed or well developed. Tibial spurs strongly pectinate (Fig. 4, H). Wing with very variable venation, the venation sometimes extremely abnormal; usually 1 to 3 cubital cells, a discoidal cell, and a radial cell that is either closed or almost closed. Body clothed with long, flexible, abundant hairs. Stipes with very blunt apex.

This subgenus contains 13 species, 7 subspecies, and 8 varieties. These are confined to the Southwestern and Western States, with the exception of *badius* (Latreille), which is distributed along the Coastal States from Louisiana into New Jersey. The males of some species appear in immense numbers during their nuptial flights. Species examined, *badius* (Latreille), *barbatus* vars. *molefaciens* (Buckley) and *nigrescens* Wheeler, *californicus* (Buckley), *comanche* Wheeler, *desertorum* Wheeler, and *occidentalis* (Cresson).

POGONOMYRMEX, subgenus EPHEBOMYRMEX Wheeler

*Pogonomyrmex* (*Epebomyrmex*) Wheeler, 1902, Psyche 9: 390.

Subgenotype, *Pogonomyrmex naegelii* Forel (by designation of Wheeler, 1911).

Characters similar to those of *Pogonomyrmex* (*Pogonomyrmex*) except that the males are smaller (4.5 mm.), the Mayrian furrows are usually very distinct, and the occipital border of the head forms a very pronounced flange.

Three species, *pima* Wheeler and *townsendi* Wheeler of Arizona and *imberbiculus* Wheeler of Oklahoma and Texas. The male has not been described for any of these species. The above description is based on males of *imberbiculus* which are in the collection of the National Museum.

STENAMMA Westwood

*Stenamma* Westwood, 1840, An Introduction to the Modern Classification of Insects, vol. 3, p. 83.

Genotype, *Stenamma westwoodi* (Stephens, M. S.) Westwood (monobasic).

Length 2.3-5 mm. Antenna 13-segmented; scape not less than combined lengths of first 3 to 5 funicular segments; first funicular segment wider than the second; funiculus noticeably enlarging toward apex but not forming a

definite club. Mandible well developed, distinctly toothed. Ocelli not placed on a prominent protuberance. Mayrian furrows usually present but sometimes absent or obsolescent. Wing with prominent stigma; no radial cell, discoidal cell usually present; usually 1 but sometimes 2 cubital cells. Epinotum somewhat depressed (*brevicorne* (Mayr) and its variants (Fig. 4, A)) or else angulate; when depressed, bearing a pair of large, blunt tubercles. Petiole rather strongly pedunculate (Fig. 4, C). Genitalia not prominent. Cerci present.

Three species, 5 subspecies, and 1 variety. Entire United States with the possible exception of the most extreme southern section. Those forms east of the Mississippi River generally belong to *brevicorne* or else are variants of it. Species examined, *brevicorne* (Mayr), *brevicorne diecki* var. *impressum* Emery, and *nearcticum* Mayr.

#### APHAENOGASTER, subgenus ATTOMYRMA Emery

*Aphaenogaster* (*Attomyrma*) Emery, 1915, Accad. delle Sci. dell'Ist di Bologna Rend. 19: 70.

Subgenotype, *Formica subterranea* Latreille (by original designation).

Length 3-5 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 3 funicular segments. Ocelli small. Mandible subtriangular, toothed. Head unusually flattened (Fig. 1, D). Mayrian furrows usually present, though sometimes indistinct or apparently wanting. Wing with well-developed stigma, 2 cubital cells, and a discoidal cell; radial cell not distinctly closed. Epinotum usually with a pair of tubercles. Legs rather slender. Cerci present.

Eleven species, 12 subspecies, and 13 varieties. Occurring throughout the United States but more common in the southern and eastern half. Specimens examined, *fulva* Roger, *fulva aquia* (Buckley), *fulva aquia* vars. *picea* Emery and *rudis* Emery, *lamellidens* var. *nigripes* M. R. Smith, *tennesseensis* (Mayr), and *treatae* Forel.

#### NOVOMESSOR Emery

*Novomessor* Emery, 1915, Accad. delle Sci. dell'Ist. di Bologna Rend. 19: 73.

Genotype, *Aphaenogaster* (*Ischnomyrmex*) *cockerelli* André (by original designation).

Length 6-7.5 mm. Antenna 13-segmented; funiculus slender, not terminating in a distinct club; scape approximately as long as combined lengths of first 3 funicular segments. Ocelli not placed on a prominent protuberance. Head narrow dorsoventrally; flat beneath, moderately convex above. Mandible well developed, with distinct masticatory border which bears only a very few, distinct teeth. Posterior border of head slightly constricted to form a weak collar or flange (Fig. 1, J). Mayrian furrows weakly developed. Epinotum in profile angular, bearing a pair of very small tubercles. Wing with prominent stigma; a cubital and a discoidal cell but no radial cell. Legs remarkably long and slender. Cerci present. Genitalia small.

Two species, *cockerelli* (André) and *albisetosus* (Mayr), which are

confined to the arid regions of Texas, New Mexico, and Arizona. *Novomessor cockerelli* appears to be the more common form. Species examined, *cockerelli*.

#### VEROMESSOR Forel

*Novomessor* (*Veromessor*) Forel, 1917, Soc. Vaud. des Sci. Nat. Bul. 51: 235.  
Genotype, *Aphaenogaster andrei* Mayr (by designation of Emery, 1921).

Length 6.5-8.5 mm. Antenna 13-segmented; scape not so long as combined lengths of first 4 funicular segments. Mandible well developed, distinctly toothed. Ocelli small. Mayrian furrow present but usually weakly developed. Wing with prominent stigma; 1 cubital and 1 discoidal cell; radial cell present or absent. Intercubitus absent or poorly developed owing to the fusion of the radial and cubital veins (*Formica* type, Fig. 5, D). Legs slender but not so remarkably long as with *Novomessor*.

Five species and 2 subspecies, one or more of which occur in Colorado, Nevada, Arizona, and California. California contains all of the 7 forms except *lobognathus* (Cockerell). Species examined, *andrei* (Mayr), *pergandei* (Mayr), and *stoddardi* (Emery).

#### PHEIDOLE, subgenus MACROPHEIDOLE Emery

*Pheidole* (*Macropheidole*) Emery, 1915, Soc. Ent. de France Bul., p. 190.  
Subgenotype, *Pheidole fimbriata* Roger (monobasic).

This subgenus is represented by a single native species, *rhea* Wheeler of Arizona, the male of which is unknown. The male of *rhea* should be easily distinguished by its size. The female, which is 14.2 mm. long, is the largest known species of *Pheidole* in the United States.

#### PHEIDOLE, subgenus PHEIDOLE Westwood

*Pheidole* Westwood, 1840, Ann. and Mag. Nat. Hist. 6: 87.

Subgenotype, (*Atta providens* Sykes) = *Pheidole indica* Mayr (by designation of Bingham, 1903).

Length 2.5-5 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 2 funicular segments; first funicular segment noticeably widened (annular or subglobular). Mandible small but with one or more teeth, usually 1 to 3. Eye large, convex, placed close to base of mandible. Ocelli borne on a high protuberance at summit of head (Fig. 1, H). Mayrian furrows usually well developed, distinct. Wing with prominent stigma; 2 cubital and a discoidal cell but usually no radial cell. Cerci present.

Forty species, 20 subspecies, and 23 varieties; one or more of these occur in every State in the Union; this subgenus is best represented, though, in the Southwestern and Western States. *P. megacephala* (F.) has been introduced into a number of localities in Florida and *anastasii* Emery has become established in greenhouses in several of our Eastern States. Species examined, *anastasii* Emery, *dentata* Mayr, *hyatti* Emery, *megacephala* (Fabricius), and *vinelandica* Forel.



## EPIPHEIDOLE Wheeler

(Fig. 7, C)

*Epipheidole* Wheeler, 1904, Amer. Mus. Nat. Hist. Bul. 20: 14.Genotype, *Epipheidole inquilina* Wheeler (monobasic).

Length 3-3.5 mm. Antenna 13-segmented; scape very short; first funicular segment noticeably enlarged; funiculus long and slender. Mandible small, slender, 2- to 3-toothed. Mayrian furrows absent. Wing with prominent stigma; 2 cubital cells but no radial or discoidal cell. Epinotum with 2 well-developed spines. Cerci present.

One species, *inquilina* Wheeler, which is parasitic in colonies of *Pheidole pilifera* (Roger) and its subspecies *coloradensis* Emery. Colorado and Nebraska. Rare. No specimens of *inquilina* have been examined.

## SYMPHEIDOLE Wheeler

(Fig. 7, E)

*Symphoidole* Wheeler, 1904, Amer. Mus. Nat. Hist. Bul. 20: 7.Genotype, *Symphoidole elecebra* Wheeler (monobasic).

Length 2.5-2.75 mm. Antenna 13-segmented; scape short; first funicular segment large, globose; funiculus long and slender. Mandible small, slender, with a single apical tooth. Mayrian furrows absent. Wing with a prominent stigma; 2 cubital and a discoidal cell, but no radial cell. Epinotum rounded, unarmed. Postpetiole much broader than long, angulate on each side. Cerci present.

One species, *elecebra* Wheeler, which is parasitic in colonies of *Pheidole ceras* Wheeler. Colorado. Rare. No specimens of *elecebra* examined.

## CARDIOCONDYLA Emery

*Cardiocondyla* Emery, 1869, Accad. degli Aspiranti, Naples Ann. 2: 21.Genotype, *Cardiocondyla elegans* Emery (monobasic).

Length 2 mm. Antenna 13-segmented; all segments longer than wide; scape long, at least as long as combined lengths of first 5 funicular segments. Mandible well developed, with distinct teeth. Prothorax with well-defined humeral angles. Mayrian furrows absent. Wing feebly veined; usually a cubital but no radial or discoidal cells; stigma distinct but not large.

One species and 2 varieties, apparently introduced, all of which occur in Florida. The male of *emeryi* Forel is normal but the males of *wroughtoni* var. *bimaculata* Forel and *nuda* var. *minutior* Forel are ergatandrous. For characters of the ergatandrous forms see the key. No males have been examined of any of these forms.

## CREMATOGASTER, subgenus ORTHOCREMA Santschi

*Crematogaster* (*Orthocrema*) Santschi, 1918, Soc. Ent. de France Bul., p. 182.Subgenotype, *Myrmica sordidula* Nylander (by original designation).

Length 2.5-3 mm. Characters similar to those of *Crematogaster*, subgenus *Acrocoelia* Mayr except that the antennae are 11-segmented.

One species and 3 subspecies, which are mostly southern in distribution. *C. minutissima missouriensis* Emery is the most common form. Males examined of *minutissima missouriensis* and *minutissima minutissima* Mayr.

#### CREMATOGASTER, subgenus ACROCOELIA Mayr

*Acrocoelia* Mayr, 1852 [1853], Zool. Bot. Gesell. Wien, Verh. 2: 146.

Subgenotype, (*Acrocoelia ruficeps* Mayr) = *Formica scutellaris* Olivier (by designation of Bingham, 1903).

Length 2.5 mm. Antenna 12-segmented; scape very short; funiculus usually with strong constrictions between the segments, which give the segments somewhat of a beadlike appearance (Fig. 2, D). Mandible elongate, masticatory border usually toothed. Mesonotum large, convex, without Mayrian furrows. Wing usually with a cubital and a discoidal cell, the veins delimiting these often very faint. Postpetiole attached to dorsal surface of base of gaster. Gaster from above usually subcordate (Fig. 6, H).

Nine species and 10 varieties; one or more of these distributed over all parts of the United States. Species examined, *ashmeadi* Mayr, *atkinsoni* Wheeler, *laeviuscula* Mayr, *lineolata* (Say), *lineolata* var. *cerasi* (Fitch), *lineolata* var. *lutescens* Emery, *lineolata* var. *subopaca* Emery, and *pilosa* Emery.

#### MONOMORIUM, subgenus MONOMORIUM Mayr

*Monomorium* Mayr, 1855, Zool.-Bot. Gesell. Wien, Verh. 5: 452.

Subgenotype, *Monomorium minus* Mayr (monobasic).

Length 2.5-4.5 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 2 funicular segments. Mandible slender, elongate, with several teeth (Fig. 2, I). No Mayrian furrows. Wing with well-developed stigma; a single cubital cell.

This subgenus contains 3 species and 1 variety, *minus* (Buckley), of the entire United States, and its variety *ergatogyna* Wheeler, of California; *floricola* (Jerdon) of Florida; and the introduced *pharaonis* (Linnaeus) of most of our larger towns and cities. Males have been examined of all these forms, except *ergatogyna*.

#### MONOMORIUM, subgenus PARHOLCOMYRMEX Emery

*Monomorium* (*Parholcomyrmex*) Emery, 1915, Soc. Ent. de France Bul., p. 190.

Subgenotype, *Myrmica gracillima* F. Smith (by original designation).

Length 4-4.5 mm. Antenna 13-segmented; scape much swollen, shorter than even the second funicular segment; first funicular segment globular, the succeeding segments gradually narrowing in width toward apex of funiculus. No Mayrian furrows. Wing with well-developed stigma; a single cubital cell; discoidal cell usually present but radial cell absent.

One introduced species, *destructor* (Jerdon), which occurs in a few southern towns and cities. The male of this species has not been examined.

#### XENOMYRMEX Forel

*Xenomyrmex* Forel, Soc. Vaud. des Sci. Nat. Bul. 20: 369.

Genotype, *Xenomyrmex stollii* Forel (monobasic).

Length 2 mm. Antenna 12-segmented; scape approximately as long as combined lengths of first 2 funicular segments; last funicular segment approximately as long as combined lengths of 2 preceding segments. Mandible longer than broad, toothed. Eye large, ocelli small. Mayrian furrows present. Wing with distinct stigma; venation greatly reduced; no radial, cubital, or discoidal cells. Posterior wing lanceolate, with long cilia-like hairs on posterior margin. Epinotum without spines or tubercles. Petiole nonpedunculate (Fig. 4, B). Legs neither long nor incrassated. Cerci present. Stipes moderately large, subtriangular in profile.

Two subspecies, *stollii rufescens* Wheeler and *stollii floridanus* Emery, both of Florida. Rare. Only males of *floridanus* have been examined.

#### SOLENOPSIS Westwood

*Solenopsis* Westwood, 1840, Ann. and Mag. Nat. Hist. 6:86.

Genotype, (*Solenopsis mandibularis* Westwood) = *Atta geminata* Fabricius (monobasic).

Length 3-6 mm. Antenna 12-segmented; scape short; first funicular segment globular or annular (Fig. 1, H); funiculus often narrowed apically. Mandible small, narrow, usually toothed. Clypeus convex. Eye very large, borne on anterior half of head. Ocelli situated on high summitlike protuberance at vertex of head (Fig. 1, H). No Mayrian furrows. Wing with distinct stigma; a cubital and a discoidal cell but no radial cell. Cerci present. Stipes fairly prominent.

This genus contains 11 species, 6 subspecies, and 6 varieties, all of which are confined to the southern half of the United States except *molesta* (Say) and its forms. Species examined, *geminata* (Fabricius) and subspecies *rufa* (Jerdon), *saevissima* var. *richteri* Forel, *molesta* (Say), *xyloxi* MacCook.

#### EPOECUS Emery

(Fig. 7, F)

*Epoecus* Emery, 1892, Soc. Ent. de France Ann. 61: 276.

Genotype, *Epoecus pergandei* Emery (monobasic).

Length 2 mm. Antenna 11- or 12-segmented; scape long, approximately as long as combined lengths of first 7 or 8 funicular segments; last 3 funicular segments noticeably larger than preceding segments. Anterior border of clypeus with a median impression and 2 teeth. Wing with a distinct stigma; a cubital but no radial or discoidal cell. According to Emery the mandible is narrow and pointed. Base of gaster with a very prominent impression above.

Only one species, *pergandei* Emery, which is probably parasitic in colonies of *Monomorium minimum* (Buckley). District of Columbia. Extremely rare. No worker caste known. Males examined.

#### ANERGATES Forel

(Fig. 7, H)

*Anergates* Forel, 1874, Schweiz. Naturf. Gesell. Denkschr. 26: 93.

Genotype, *Myrmica atratula* Schenck (monobasic).

Length 2.5-3 mm. Wingless. Pupoid. Antenna 11-segmented. Clypeus emarginate. Mandible edentate. Mayrian furrows absent. Petiole and postpetiole very short and broad. Gaster convex above, concave beneath, with apex directed anteroventrally. Genitalia large and prominent.

Parasitic in colonies of *Tetramorium caespitum* (Linnaeus). Apparently only one species, *atratus* (Schenck). Extremely rare. Delaware, New Jersey, and Virginia. No males examined.

#### EREBOMYRMA Wheeler

(Fig. 7, C)

*Erebomyrma* Wheeler, 1903, Biol. Bul. 4: 138.

Genotype, *Erebomyrma longi* Wheeler (monobasic).

Length 5-5.5 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 2 funicular segments; funiculus subfiliform. Mandible well developed, with 4 teeth. Clypeus strongly convex. Thorax without definite Mayrian furrows but with faint parapsidal sutures. Wing with a well-developed stigma; a cubital, a radial, and a discoidal cell; brownish, with apical third hyaline. Petiole scarcely pedunculate. Cerci present.

Only one species, *longi*, Wheeler of northern Texas. Males examined.

#### MYRMECINA Curtis

*Myrmecina* Curtis, 1829, Brit. Ent. 6: 265.

Genotype, (*Myrmecina latreillei* Curtis) = *Formica graminicola* Latreille (monobasic).

Length 3-4 mm. Antenna 13-segmented; scape rather short, but distinctly longer than second funicular segment; funiculus enlarged apically but not forming a definite club, the constrictions between the funicular segments very distinct. Mandible vestigial, represented by a blunt, toothless stub (Fig. 2, E). Labrum exposed. Ocelli small. Mayrian furrows distinct. Wing dark, pilose, with ciliated margins; stigma distinct; a radial and cubital cell but no discoidal cell; radial cell usually appendiculate (Fig. 5, C). Middle of femur and tibia noticeably incrassated. Epinotum with a pair of spines or tubercles. Petiole and postpetiole very suggestive of that of the worker. Genitalia often retracted. Cerci present.

Two subspecies and one variety. The subspecies, *graminicola americana*

Emery, is the most common form. Ants of this genus occur over almost the entire United States, at least as far west as Arizona and Montana; they are apparently more common, though, in the eastern half. Males of *graminicola americana* examined.

#### MACROMISCHA Roger

*Macromischa* Roger, 1863, Berlin Ent. Ztschr. 7: 184.

Genotype, *Macromischa purpurata* Roger (by designation of Wheeler, 1911).

Length 2-3 mm. Antenna 13-segmented; scape unusually long and slender, approximately as long as combined lengths of first 9 or 10 funicular segments; last 3 funicular segments noticeably enlarged. Mandible small but distinctly toothed. No definite Mayrian furrows. Wing with faint veins; a well-developed stigma but no radial, cubital, or discoidal cells. Scutellum strongly convex. Gaster with distinct basal angles. Uncommon.

Three species, *floridanus* (Wheeler) of Florida, *polita* M. R. Smith of Arizona, and *subditiva* Wheeler of Texas. Description based on males of *subditiva*.

#### LEPTOTHORAX, subgenus LEPTOTHORAX Mayr

*Leptothorax* Mayr, 1855, Zool.-Bot. Gesell. Wien, Verh. 5: 431.

Subgenotype, *Myrmica clypeata* Mayr (by designation of Emery, 1912).

Length 2-4 mm. Antenna 12- or 13-segmented, usually with a well-differentiated club. Mayrian furrows present but often not clearly defined. Wing with a distinct stigma; a single cubital cell; radial and discoidal cell present or absent.

Twenty-one species, 6 subspecies, and 7 varieties. One or more forms occur in every section of the United States. Species examined, *curvispinosus* Mayr and *longispinosus* Roger.

#### LEPTOTHORAX, subgenus DICHOTHORAX Emery

*Leptothorax* (*Dichothorax*) Emery, 1895, Zool. Jahrb. Abt. f. System. 8: 323.

Subgenotype, *Leptothorax* (*Dichothorax*) *pergandei* Emery (by designation of Wheeler, 1911).

Length 2-2.5 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 5 funicular segments; first funicular segments noticeably wider than second; funicular segments 2 to 8 very slender; last 4 funicular segments forming a club, the last segment of which is longer than the 2 preceding segments. Mandible with 4 teeth. Eye very convex, placed near base of mandible. Head somewhat flattened. Mesonotum large, without Mayrian furrows. Wing with well-developed stigma; a cubital cell but no radial or discoidal cells; hyaline with pale veins. Hairs simple.

One species, 2 subspecies, and 1 variety, which are either *pergandei* Emery or variants of this species. Distributed from Florida and Virginia westward to at least Iowa and Texas. Males of *pergandei* examined.

## LEPTOTHORAX, subgenus MYCHOTHORAX Ruzsky

*Leptothorax (Mychothorax)* Ruzsky, 1904, Fourmis Gouv. Arkangelsk Bul. Soc. Geogr., p. 228.

Subgenotype, *Formica acervorum* Fabricius (by designation of Wheeler, 1911).

Length 3-4 mm. Antenna 12-segmented; scape approximately as long as combined lengths of first 2 funicular segments; no distinct antennal club. Mayrian furrows well developed. Wing with distinct stigma; no radial cell but a cubital and a discoidal cell. Petiole and postpetiole usually rather robust. Cerci present.

Five species, 5 subspecies, and 6 varieties, which are distributed over the northern half of the United States, especially the North and Northwest. Species examined, *acervorum canadensis* Provancher, *acervorum canadensis* var. *calderoni* Forel, *duloticus* Wesson, *emersoni* Wheeler, *muscorum* var. *septentrionalis* Wheeler, and the ergatandrous males of *diversipilosus* M. R. Smith.

## SYMMYRMICA Wheeler

(Fig. 7. A)

*Symmyrmica* Wheeler, 1904, Amer. Mus. Nat. Hist. Bul. 20: 3.

Genotype, *Symmyrmica chamberlini* Wheeler (monobasic).

Length 3-3.25 mm. Wingless. Ergatandrous. Antenna 11-segmented. Eye and ocellus very large and prominent. Mandible small, not meeting, each with a single acute tooth on masticatory border. Clypeus short, very convex. Mayrian furrows feebly developed. Epinotum with a pair of obtuse swellings. Cerci present. Gaster and genitalia not especially large.

One species, *chamberlini* Wheeler. Inquilinous in colonies of *Myrmica mutica* Emery. Extremely rare. Utah. No males of this species have been examined.

## HARPAGOXENUS Forel

*Tomognathus* Mayr, 1861, Die Europäischen Formiciden, p. 56 (preoccupied by Agassiz, 1850).

*Harpagoxenus* Forel, 1893, Soc. Ent. de Belg. Ann. 37: 167.

Genotype, *Myrmica sublaevis* Nylander.

Length 2.7 mm. Antenna 12-segmented; scape long, approximately as long as combined lengths of first 5 funicular segments. Mandible well developed, usually distinctly toothed. Antennal scrobe weakly to moderately well developed, extending posteriorly on head approximately to ocelli (Fig. 1, F). Mayrian furrows and parapsidal sutures present. Wing with cubital cell but no radial cell; discoidal cell present or absent; stigma well developed but often pale. Mandibles, antennae, wings, and legs exceedingly pale.

Two species, *americanus* Emery and *canadensis* M. R. Smith. The former is a slave-making form on *Leptothorax longispinosus* Roger and *L. curvispinosus* Mayr. The species has been collected in Virginia, New Jersey, Massachusetts, New York, Pennsylvania, Illinois, and Ohio. *Harpagoxenus canadensis*,

which was originally described from Quebec, Canada, has recently been collected in Minnesota. This ant is a slave-making form on *Leptothorax acervorum canadensis* Provancher var. Only the male of *americanus* is known. The characters of the male *canadensis* should prove similar to those of the European *sublaevis* Nylander. Males of *americanus* examined.

#### TRIGLYPHOTHRIX Forel

*Triglyphothrix* Forel, 1890, Soc. Ent. de Belg. Comp. Rend. 34: cvi.

Genotype, *Triglyphothrix walshi* Forel (monobasic).

Similar to *Tetramorium* except in bearing trifold or branched hairs (Fig. 6, F), at least in part. Introduced.

One species, *striatidens* (Emery) occurs in several towns in Florida, South Carolina, Alabama, Mississippi, and Louisiana. The male of *striatidens* is unknown; it will probably measure approximately 2.75-3.75 mm. in length.

#### TETRAMORIUM Mayr

*Tetramorium* Mayr, 1855, Zool.-Bot. Gesell. Wien, Verh. 5: 423.

Genotype, *Formica caespitum* Linnaeus (by designation of Girard, 1879).

Length 2.6-7 mm. Antenna 10-segmented; second funicular segment unusually long, closely approximating length of scape (Fig. 1, I). Mandible well developed, toothed. Mayrian furrows present. Wing with a cubital and a discoidal cell, the radial cell present or absent. Legs slender. Hairs simple.

Four species, all introduced; usually found in towns and cities or their immediate vicinities, especially the more important seaport and railroad points in the southern and eastern half of the United States. According to their relative abundance the species might be ranked as follows: *caespitum* (Linnaeus), *guineense* (Fabricius), *simillimum* (F. Smith), and a form of the *pacificum* Mayr group. Males have been examined of all these species.

#### XIPHOMYRMEX Forel

*Tetramorium* (*Xiphomyrmex*) Forel, 1887, Schweiz. Ent. Ges. Mitt. 7: 385.

Genotype, *Tetramorium* (*Xiphomyrmex*) *kelleri* Forel (by designation of Wheeler, 1911).

Characters same as for *Tetramorium*.

Native. Habitat, very warm, dry, open regions. Two subspecies, *spinosus hispidus* Wheeler of the desert region around Tucson and Phoenix, Ariz., and *spinosus insons* Wheeler from localities in Texas and Arizona. Males of both subspecies are unknown; they will probably range from 4-6 mm. in length.

#### WASMANNIA Forel

*Wasmannia* Forel, 1893, Ent. Soc. Lond. Trans., p. 383.

Genotype, *Tetramorium auropunctatum* Roger (by designation of Wheeler, 1911).



Length 4.5 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 2 funicular segments; first funicular segment pyriform; funiculus rather long and slender. Eye large, convex, protuberant. Mandible well developed, subtriangular, distinctly toothed. Clypeus convex. Mayrian furrows and parapsidal sutures present. Wing with prominent stigma; a cubital but no radial or discoidal cells. Cerci present. Stipes long, very slender, with a prominent inner basal tooth (Fig. 6, *E*). Hypopygium terminating apically in a point.

One introduced species, *auropunctata* (Roger), which occurs in a number of localities in Florida. Males examined.

#### CRYPTOCERUS, subgenus CRYPTOCERUS Fabricius

*Cryptocerus* Fabricius, 1804, *Systema Piezatorum*, p. 418.

Subgenotype, *Cryptocerus umbraculatus* Fabricius (by designation of Emery, 1914).

Length 5 mm. or less. Antenna 13-segmented; funiculus greatly thickened toward apex, clavate (Fig. 2, *B*); scape shorter than second funicular segment; first funicular segment small; last 4 funicular segments greatly enlarged forming somewhat of a club. Mandible well developed, subtriangular, toothed. Mayrian furrows present. Wing with a distinct stigma; a radial, a cubital, and a discoidal cell; radial cell rather short, appendiculate, the appendix sometimes vestigial (Fig. 5, *C*). Legs rather short, femora somewhat incrassated. Cerci present. Stipes prominent.

Two species, *rohweri* Wheeler, of Arizona, and *texasus* Santschi, of Texas. No males have been examined of either species.

#### CRYPTOCERUS, subgenus CYATHOMYRMEX Creighton

*Cryptocerus* (*Cyathocephalus*) Emery, 1915, *Soc. Ent. de France Bul.*, p. 192 (pre-occupied by Kessler, 1868).

*Cyathomyrmex* Creighton, 1933, *Psyche*, 40: 98.

Subgenotype, *Cryptocerus pallens* Klug (by original designation).

Characters same as for *Cryptocerus*, subgenus *Cryptocerus*.

One species, *varians* F. Smith, of Florida. No males examined.

#### STRUMIGENYS, subgenus STRUMIGENYS F. Smith

*Strumigenys* F. Smith, 1860, *Jour. Ent.* 1: 72 [London].

Subgenotype, *Strumigenys mandibularis* F. Smith (monobasic).

Length 2-3 mm. Head much narrowed toward the mandibles. Antenna 13-segmented; scape short; funiculus long, subfiliform. Mandible narrow, much longer than broad, toothed or toothless. Eye convex, strongly protuberant. Mayrian furrows present. Wing pilose, with ciliated margins; veins poorly developed, indistinct, especially in apical half of wing; a single cubital cell present. Declivity of epinotum somewhat laterally margined, especially in lower half. Petiole and postpetiole often with thin, membranous appendages beneath and around margins.



Uncommon. *Strumigenys louisianae* Roger and its subspecies *laticephala* M. R. Smith are both distinctly southern. Males of each have been examined.

#### STRUMIGENYS, subgenus TRICHOSCAPA Emery

*Cephaloxys* F. Smith, 1864, Linn. Soc. Lond. Jour. Zool. 8: 76 (preoccupied by Signoret, 1847).

Genotype, *Cephaloxys capitata* F. Smith (monobasic).

*Strumigenys* (*Trichoscapa*) Emery, 1869, Accad. degli Aspiranti Naples Ann. 2: 24.

Subgenotype, *Strumigenys* (*Trichoscapa*) *membranifera* Emery (monobasic).

Characters same as for *Strumigenys*, subgenus *Strumigenys*.

Uncommon. Twenty species, 1 subspecies, and 4 varieties. Members of this subgenus are confined mostly to the eastern half of the United States. Species examined, *pergandei* Emery, *pulchella* Emery, *rostrata* Emery, *venatrix* Wesson and Wesson, and *reflexa* Wesson and Wesson.

The usage of *Trichoscapa* was formerly suppressed in favor of the earlier name *Cephaloxys*. Since *Cephaloxys* is preoccupied as indicated above, it will be necessary to revert again to the use of the name *Trichoscapa*.

#### CYPHOMYRMEX, subgenus CYPHOMYRMEX Mayr

*Cyphomyrmex* Mayr, 1862, Zool.-Bot. Gesell. Wien, Verh. 12: 690.

Subgenotype, *Cryptocerus rimosus* Spinola (by designation of Wheeler, 1911).

Length 2.3-2.6 mm. Antenna 13-segmented; scape very long, approximately as long as combined lengths of first 8 funicular segments; funiculus gradually enlarging apically but not forming a distinct club. Eye convex, protuberant. Ocelli small. Mandible large, subtriangular, toothed. Frontal carinae very large, unusually elevated (Fig. 1, B). Mayrian furrows present. Wing with stigma absent or obsolescent; a radial and 2 cubital cells present but no discoidal cell; radial cell approximately 3 times as long as broad. Legs not slender as with *Trachymyrmex*. Genitalia not prominent. Hairs on body simple.

One species, 1 subspecies, and a variety, at least one form of which is confined to Florida, Texas, or California. Species examined, *rimosus minutus* Mayr.

#### CYPHOMYRMEX, subgenus MYCETOSORITIS Wheeler

*Atta* (*Mycetosoritis*) Wheeler, 1907, Amer. Mus. Nat. Hist. Bul. 23: 714.

Subgenotype, *Atta* (*Mycetosoritis*) *hartmanni* Wheeler (monobasic).

Length 2 mm. Characters similar to those of *Cyphomyrmex*, subgenus *Cyphomyrmex*, except that the body hairs are curved or hooked instead of simple.

A single species, *hartmanni* Wheeler of Texas. No specimens of *hartmanni* have been examined.

#### TRACHYMYRMEX Forel

*Atta* (*Trachymyrmex*) Forel, 1893, Soc. Ent. de Belg. Ann. 37:600.

Genotype, *Atta septentrionalis* McCook (by designation of Wheeler, 1911).

Length 3-5 mm. Antenna 13-segmented; scape long, approximately as long as combined lengths of first 8 funicular segments; funiculus enlarged apically, the last 4 segments forming a rather distinct club. Eye convex, protuberant. Ocelli very small. Mandible large, subtriangular, toothed, the teeth often small. Mayrian furrows and parapsidal sutures present, the former not always clearly defined. Wing with distinct but not large stigma; a radial and a cubital cell present but no discoidal cell; radial cell approximately 3 times as long as broad. Epinotum with a pair of distinct spines. Legs exceedingly slender. Genitalia not especially prominent.

Four species, 2 subspecies, and 4 varieties; 6 of the 10 forms belong to *septentrionalis* (McCook). Distributed over the eastern half of the United States and several of the extreme Southwestern States. Species examined, *arizonensis* Wheeler and *septentrionalis* (McCook).

#### ACROMYRMEX, subgenus MOELLERIUS Forel

*Atta* (Moellerius) Forel, 1893, Soc. Ent. de Belg. Ann. 37: 589.

Subgenotype, *Atta* (*Acromyrmex*) *landolti* Forel (by designation of Wheeler, 1911).

Length 8 mm. Antenna 13-segmented; scape very long, approximately as long as combined lengths of first 8 funicular segments; funiculus noticeably enlarging toward apex. Eye convex, very protuberant. Ocelli small. Mandible large, subtriangular, with well-developed teeth (Fig. 2, F). Mayrian furrows present but not always clearly defined; parapsidal sutures present. Wing with well-developed veins; stigma distinct but small; a radial and a cubital cell present but no discoidal cell; radial cell approximately 3 times as long as broad. Legs slender. Dorsal surface of first gastric segment with a depression on each side near base and a median depression more posteriorly. Stipes large, stout, inwardly curved, with inner basal tooth and truncate apex (Fig. 6, G).

One species, *versicolor* (Pergande) of Arizona, and the subspecies, *chisosensis* Wheeler of Texas. Species examined, *versicolor* (Pergande).

#### ATTA Fabricius

*Atta* Fabricius, 1804, System Piezatorum, p. 421.

Genotype, *Formica cephalotes* Linnaeus (by designation of Wheeler, 1911).

Length 12 mm. Head unusually small in proportion to body. Mandible large, subtriangular, with numerous well-developed teeth (Fig. 2, F). Antenna 13-segmented; scape very long, approximately as long as combined lengths of first 8 funicular segments; funiculus noticeably enlarged apically. Ocelli large, strongly protuberant. Thorax unusually large. Mayrian furrows absent or obsolescent. Wing with well-developed veins; no distinct stigma; a radial and a cubital cell present but no discoidal cell; radial cell at least 6 times as long as broad. Legs exceedingly slender. Genitalia large, with pronounced characteristic configuration.

One species, *texana* Buckley of Texas and western Louisiana. Species examined, *texana* Buckley.

## Subfamilies DOLICHODERINAE Forel and FORMICINAE Lepeletier

(Note: The symbol D, in parenthesis, refers to the subfamily *Dolichoderinae* and the symbol F to the subfamily *Formicinae*.)

1. Antenna 10-segmented; length of body 1-2 mm. or slightly more .....  
*Brachymyrmex*, subgenus *Brachymyrmex* Mayr (F), p. 313  
 Antenna with more than 10 segments; size usually larger ..... 2
2. (1) Mandible elongate, slender, somewhat sickle-shaped, and without masticatory border of teeth (Fig. 2, C).....*Polyergus* Latreille (F), p. 320  
 Mandible not as described above, usually with distinct masticatory border.... 3
3. (2) Scape approximately as long as the combined lengths of the first 3 funicular segments or longer ..... 7  
 Scape shorter than the combined lengths of the first 3 funicular segments; if not, then the head is flattened (Fig. 1, D), and the third segment of the maxillary palpus is approximately as long as the combined lengths of segments 4, 5, and 6 ..... 4
4. (3) Radial cell narrow and open; no discoidal cell ..... 5  
 Radial cell closed or open; usually a discoidal cell ..... 6
5. (4) Third segment of maxillary palpus much longer than the second segment, approximately as long as the combined lengths of segments 4, 5, and 6; (head flattened (fig. 1, D), strongly concave beneath; anterior part of thorax often strongly protuberant; New Jersey to Iowa and California and southward) .....*Dorymyrmex* Mayr (D), p. 312  
 Third segment of maxillary palpus about as long as the second segment and much shorter than the combined lengths of the fourth, fifth, and sixth segments .....*Forelius* Emery (D), p. 312
6. (4) Second funicular segment remarkably long, very distinctly longer than scape; (introduced species).....*Iridomyrmex* Mayr (part) (D), p. 311  
 Second funicular segment at most not exceeding length of antennal scape; (mandible well developed, subtriangular, with distinct masticatory border bearing numerous denticulae (fig. 2, H); integument rather highly sclerotized; petiole stout, thick anterioposteriorly; Eastern States and westward to Minnesota and Oklahoma) .....  
*Dolichoderus*, subgenus *Hypoclinea* Mayr (D), p. 310
7. (3) Scape usually shorter than combined lengths of first 4 funicular segments; if not, then the petiole is inclined, and the base of the gaster is impressed (fig. 3, B) ..... 8  
 Scape usually longer than combined lengths of first 4 funicular segments; of not, then the petiole is not inclined, and the base of the gaster is not impressed ..... 10
8. (7) Genital appendages unusually large, comprising at least one-third of the gaster (fig. 3, E); wing normally with 2 cubital cells, a radial cell and a discoidal cell; mandible large, subtriangular, and bearing numerous teeth or denticulae (fig. 2, H); (Southwestern and Western States); 7-10 mm. long .....*Liometopum* Mayr (D), p. 311  
 Genital appendages not so large and prominent as described above; wing normally with less than 2 cubital cells; mandible smaller; 5 mm. or less in length ..... 9
9. (8) Petiole inclined, thick anteroposteriorly; base of gaster with a distinct, wedge-shaped impression (fig. 3, B).....*Prenolepis* Mayr (F), p. 317  
 Petiole erect, not inclined or noticeably thick antero-posteriorly; base of gaster without a distinct wedge-shaped impression; (native species).....  
*Iridomyrmex* Mayr (part) (D), p. 311

10. (7) Antenna often inserted some distance from posterior border of clypeus; clypeal suture separated from antennal fossa; large ants usually 5 mm. or more in length; stipes prominent, moderately long and slender (fig. 3, C) ..... *Camponotus*, subgenera *Camponotus* Mayr, p. 313; *Tanaemyrmex* Ashmead, p. 314; *Myrmothrix* Forel, p. 314; *Colobopsis* Mayr, p. 315; *Myrmaphaenus* Emery, p. 315; *Manniella* Wheeler, p. 315; *Myrmobrachys* Forel, p. 315.  
 Antenna usually inserted at posterior border of clypeus or in very close proximity to posterior border of clypeus (fig. 1, A) ..... 11
11. (10) Base of gaster always impressed; petiole strongly inclined (fig. 3, B); cerci small and inconspicuous, or absent ..... 12  
 Base of gaster usually not impressed; petiole not strongly inclined (suberect to erect); cerci more or less apparent ..... 14
12. (11) Scape unusually long, approximately  $1\frac{3}{4}$  times or more the length of the head; (no erect hairs on the antennal scape) ..... *Paratrechina* subgenus *Paratrechina* Motschoulsky (F), p. 316  
 Scape often exceeding the length of the head but not so long as described above ..... 13
13. (12) Tibiae, and usually scapes, with coarse, dark, suberect to erect hairs.....  
 ..... *Paratrechina*, subgenus *Nylanderia* Emery (F), p. 316  
 Tibiae and scapes without dark, suberect to erect hairs; (mandible with numerous denticulae (fig. 2, H), these sometimes very difficult to see except under high magnification)..... *Tapinoma* Förster (D), p. 313
14. (11) First segment of funiculus usually distinctly pyriform, wider than the following segment; genital appendages small or moderate in size, with their apices not directed strongly ventrad ..... 15  
 First segment of funiculus not distinctly pyriform; genital appendages rather large and robust, and usually with their apices directed strongly ventrad (fig. 3, C); (fourth segment of maxillary palpus not longer than the combined lengths of the fifth and sixth segments)..... *Formica*, subgenera *Proformica* Ruzsky, p. 319; *Neoformica* Wheeler, p. 319; *Formica* Linnaeus, p. 319.
15. (14) Maxillary palpus unusually long and slender, fourth segment longer than combined lengths of fifth and sixth segments (fig. 6, B); (Western and Southwestern States) ..... *Myrmecocystus* Wesmæl (F), p. 318  
 Maxillary palpus not unusually long and slender, the fourth segment, when present, shorter than, or equal to, combined lengths of fifth and sixth segments ..... 16
16. (15) Maxillary palpus very short, 3-segmented.....  
 ..... *Lasius*, subgenus *Acanthomyops* Mayr (F), p. 318  
 Maxillary palpus longer, 6-segmented ..... *Lasius*, subgenera *Lasius* Fabricius (F), p. 317, and *Chthonolasius* Ruzsky (F), p. 318

### Subfamily DOLICHODERINAE Forel

#### DOLICHODERUS, subgenus HYPOCLINEA Mayr

*Hypoclinea* Mayr, 1855, Zool.-Bot. Gesell. Wien, Verh. 5: 377.

Subgenotype, *Formica quadripunctata* Linnaeus (by designation of Wheeler, 1911).

Length 3.5-5.5mm. Integument rather highly sclerotized, not very flexible. Antenna 13-segmented; scape usually very slightly shorter than combined lengths of first 2 funicular segments, or at least very closely approximating

their combined lengths; second funicular segment clearly longer than the preceding or succeeding segment. Mandible well developed, subtriangular, multidenticulate (Fig. 2, *H*). Eye large, strongly convex, subreniform. Maxillary palpus rather long and slender. Parapsidal sutures present but no Mayrian furrows. Wing with well developed stigma; 1 or 2 cubital cells (usually 2), a radial cell and a discoidal cell. Petiole thick anteroposteriorly, stout, erect. Stipes short, stout.

Three species, 2 subspecies, and 4 varieties. The 3 species are *mariae* Forel, *plagiatus* Mayr, and *taschenbergi* Mayr, each of which has one or more subspecies or varieties. There are no records of any species having been collected west of the 104th degree of longitude. Species examined, *mariae* Forel and *taschenbergi* Forel.

#### LIOMETOPUM Mayr

*Liometopum* Mayr, 1861, Die Europäischen Formiciden, p. 38.

Genotype, *Formica microcephala* Panzer (monobasic).

Length 7-10.5 mm. Head small, subtriangular. Antenna 13-segmented; scape shorter than combined lengths of first 3 funicular segments. Mandible rather large, subtriangular, multidenticulate (Fig. 2, *H*). Eye longer than broad, rather strongly convex. Parapsidal sutures present but no Mayrian furrows. Wing with well-developed stigma; a radial, 2 cubital, and a discoidal cell. Petiole, in profile, cuneate, with very thin, usually emarginate superior border. Genital appendages extremely large, occupying one-third or more of gaster (Fig. 3, *E*). Cerci prominent. Body covered with fairly dense to dense pubescence, and with rather abundant, long, erect hairs.

Two species and 1 subspecies; one or more of these have been found in the following States: Texas, New Mexico, Arizona, Colorado, California, and Oregon. *Liometopum occidentale* Emery seems to be the most common form in California. Species examined, *apiculatum luctuosum* Wheeler.

#### IRIDOMYRMEX Mayr

*Iridomyrmex* Mayr, 1862, Zool.-Bot. Gesell. Wien, Verh. 12: 702.

Genotype, *Formica detecta* F. Smith (by designation of Bingham, 1903).

Length 2-3 mm. Antenna 13-segmented; scape shorter than second funicular segment (*humilis* Mayr and *iniquus* var. *nigella* Emery) or else approximately as long as, or longer than, combined lengths of first 3 funicular segments. Head flattened, often concave beneath (Fig. 1, *D*). Mandible usually distinctly toothed or else with many small denticulae. Eye moderately to very large and convex, placed near base of mandible. Thorax moderately to quite massive. Mesonotum stout, strongly convex, projecting anteriorly, with weakly defined to well defined parapsidal sutures. Wing with highly variable venation; stigma distinct but varying from small to large; radial cell present or absent, either cubital or discoidal cell, or both present. Petiole low, erect, distinct. Genital appendages small to moderately large.

Two species and 3 varieties, *Iridomyrmex humilis* Mayr, an introduced species, occurs in the Southern States and California; another introduced species, *iniquus* var. *nigella* Emery, is found at least in greenhouses throughout the eastern half of the United States; the native *pruinus* (Roger) and its variety *analis* André are confined mostly to the Southern States. Species examined, *humilis* Mayr, *iniquus* var. *nigella* Emery, and *pruinus* var. *analis* André.

#### FORELIUS Emery

*Forelius* Emery, 1888, Ztschr. f. Wiss. Zool. 46: 389.

Genotype, *Iridomyrmex maccooki* Forel (monobasic).

Length 3 mm. Antenna 13-segmented. No Mayrian furrows. Emery (1912, Wytsman's Genera Insectorum Fascicule 137: 18, 35) states that the third segment of the maxillary palpus is almost equal to the length of the second (only slightly longer) and is much shorter than the combined lengths of segments 4, 5, and 6. He is also authority for the statement that there is no radial or discoidal cell. He remarks that the ants have a strong resemblance to *Dorymyrmex*. Mayr (1886, Zool. Bot. Gesell. Wien, Verh. 36: 432) says that the petiole of *maccooki* is almost nodelike and nearly twice as broad as thick; the legs long and slender, and the wings with a closed cubital cell.

This genus is not well known in the United States. The workers, at least, resemble the workers of *Iridomyrmex* more than those of any other North American genus. Only a single species, *maccooki* (Forel), of Texas, has been described. No males of this species have been studied.

#### DORYMYRMEX Mayr

*Dorymyrmex* Mayr, 1866, Akad. der Wiss. Wien, Math. Nat. Kl. Sitzber. 53: 494.

Genotype. (*Dorymyrmex flavescens* Mayr, nec Fabricius) = *Dorymyrmex planidens* Mayr (monobasic).

Length 2-3 mm. Head flattened (Fig. 1, D), strongly concave beneath. Antenna 13-segmented; scape often shorter than combined lengths of first 2 to 3 funicular segments: all funicular segments longer than broad, first funicular segment broader than second segment. Mandible slender, with an obliquely sloping masticatory border which bears a very long apical tooth and several smaller teeth. Ocelli not placed on a prominent protuberance at summit of head. Eye large, not much longer than broad, placed rather close to base of mandible. Third segment of maxillary palpus approximately as long as combined lengths of segments 4, 5, and 6. No Mayrian furrows. Venation highly variable; a distinct stigma; no radial, cubital, or discoidal cells; usually, however, there is a vestige of a radial and often of a cubital cell. Petiole low, erect, usually thick anteroposteriorly, with rounded, nonemarginate, superior border. Legs long, slender. Cerci present. Genital appendages rather prominent.

One species, *pyramicus* (Roger) and 4 varieties. These ants occur throughout the southern two-thirds of the United States. Species examined, *pyramicus* (Roger) and its variety *bicolor* Wheeler.

## TAPINOMA Förster

*Tapinoma* Förster, 1850, Hymenopterologische Studien, vol. 1, p. 43.

Genotype, (*Tapinoma collina* Förster) = *Formica erratica* Latreille (monobasic).

Length 1.3-4.5 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 5 funicular segments or less; all funicular segments longer than broad; antennal fossa contiguous with posterior border of clypeus (Fig. 1, A). Mandible well developed, multidenticulate (Fig. 2, H), the denticulae often extremely small and difficult to see except under high magnification. Anterior border of clypeus with or without median emargination. Eyes oval, strongly convex, not touching base of mandible. Mayrian furrows absent. Wing with well-developed stigma; a radial and a cubital cell; discoidal cell present or absent. Petiole low, stout, inclined. Base of gaster with an impressed area for reception of petiole (Fig. 3, B). Genital appendages rather prominent. Stipes stout, subtriangular. Cerci present but usually small. Erect hairs on body rather sparse.

Three species, *littorale* Wheeler and the introduced *melanocephalum* (Fabricius), which occur in Florida, and the common *sessile* (Say), which is apparently distributed over the entire United States. Males have been examined of all three species.

## Subfamily FORMICINAE Lepeletier

## BRACHYMYRMEX, subgenus BRACHYMYRMEX Mayr

*Brachymyrmex* Mayr, 1868, Soc. dei Nat. di Modena Ann. 3: 163.

Subgenotype, *Brachymyrmex patagonicus* Mayr (monobasic).

Length 1-2 mm. Very small and robust. Antenna 10-segmented; scape approximately as long as combined lengths of first 5 or 6 funicular segments, first funicular segment distinctly broader than second. Head and clypeus each broader than long. Mandible vestigial, narrow and pointed, without definite masticatory border. Ocelli placed at summit of head. No Mayrian furrows. Wing with distinct stigma; a single cubital cell but no discoidal or radial cell. Petiole low, sometimes more or less obscured by junction of thorax and gaster.

One species and 2 subspecies, *nanellus* Wheeler of Texas, *heeri obscurior* Forel of Florida, and the common *heeri depilis* Emery of at least the eastern half of the United States. Species examined, *heeri depilis* Emery.

## CAMPONOTUS, subgenus CAMPONOTUS Mayr

*Camponotus* Mayr, 1861, Die Europäischen Formiciden, p. 35.

Subgenotype, *Formica ligniperda* Latreille (by designation of Bingham, 1903).

Length 8-11 mm. Head usually small. Antenna 13-segmented; scape slender, as long as, or longer than, combined lengths of first 6 funicular segments; first funicular segment noticeably wider than second. Antennal fossa distinctly separated from posterior border of clypeus. Clypeus generally subtrapezoidal.



Eye usually prominent, moderately to strongly convex, far removed from base of mandible. Mandible generally well developed, with usually a distinct apical tooth and remainder of masticatory border toothless. Cheeks long. Parapsidal sutures present but no Mayrian furrows. Wing with well-developed stigma; a radial and a cubital cell but no discoidal cell. Petiole low, usually well developed, erect, and cuneate in profile, superior border often excised. Genital appendages small. Stipes long, slender, narrowest apically (Fig. 3, G). Cerci present.

This subgenus contains 6 species, 8 subspecies, and 16 varieties. Distributed over the entire United States. There are 6 forms of *herculeanus* (Linnaeus) and 14 forms of *sansabeanus* (Buckley). The best known species of this subgenus is probably *herculeanus pennsylvanicus* (DeGeer). Species examined, *castaneus* (Latreille), *castaneus americanus* Mayr, *herculeanus ligniperdus noveboracensis* (Fitch), *herculeanus* var. *modoc* Wheeler, *herculeanus pennsylvanicus* (DeGeer), *herculeanus pennsylvanicus ferrugineus* (Fabricius), *herculeanus* var. *whymperi* Forel, *laevigatus* (F. Smith), *sansabeanus* (Buckley), *sansabeanus* var. *luteangulus* Wheeler, *sansabeanus* var. *nitidiventris* Emery, *sansabeanus* var. *semitestaceus* Emery, and *vafer* Wheeler.

#### CAMPONOTUS, subgenus TANAEMYRMEX Ashmead

*Tanaemyrmex* Ashmead, 1905, Canad. Ent. 37: 384.

Subgenotype, *Formica longipes* Gerstäcker (by designation of Emery, 1925).

Length 6.9 mm. Characters similar to those of the subgenus *Camponotus*.

Three species and 4 varieties which are distributed in the extreme southern section of the United States from North Carolina westward into Texas and Arizona. The two best known members are *socius* Roger of Florida, Georgia, South Carolina, North Carolina, Alabama, and Mississippi, and *fumidus* var. *festinatus* (Buckley) of Texas. Species examined, *tortuganus* Emery, *fumidus* var. *festinatus* (Buckley), and *fumidus* var. *fragilis* Pergande.

#### CAMPONOTUS, subgenus MYRMOTHRIX Forel

*Camponotus* (*Myrmothrix*) Forel, 1912, Soc. Ent. de Belg. Mém. 20: 91.

Subgenotype, *Formica abdominalis* Fabricius (by designation of Wheeler, 1913).

Length 6.7 mm. Characters same as for the subgenus *Camponotus*.

*Myrmothrix* contains two subspecies, *abdominalis floridanus* (Buckley), of Florida, Georgia, and South Carolina, and *abdominalis transvectus* Wheeler of Texas. Species examined, *abdominalis floridanus* (Buckley).

#### CAMPONOTUS, subgenus MYRMENTOMA Forel

*Camponotus* (*Myrmentoma*) Forel, 1912, Soc. Ent. de Belg. Mém. 20: 92.

Subgenotype, *Formica lateralis* Olivier (by designation of Wheeler, 1913).

Length 5.5-9 mm. Characters similar to those of the subgenus *Camponotus*.

One of the largest subgenera of *Camponotus* with representatives in all parts of the United States. The subgenus is badly in need of revision; at the present it is considered to have 6 species, 4 subspecies, and 10 varieties, 13 forms of which are allied to *caryae* (Fitch). Species examined, *caryae* (Fitch), *caryae* var. *decepiens* Emery, *caryae* *discolor* (Buckley), *caryae* *discolor* *clarithorax* Emery, *caryae* var. *minutus* Emery, *caryae* *rasilis* Wheeler, *caryae* *rasilis* *pavidus* Wheeler, *caryae* *subbarbatus* Emery, and *sayi* *californica* Pergande.

#### CAMPONOTUS, subgenus COLOBOPSIS Mayr

*Colobopsis* Mayr, 1861, Die Europäischen Formiciden, p. 38.

Subgenotype, *Formica truncata* Spinola (monobasic).

Length 3.7-4.5 mm. Characters similar to those of subgenus *Camponotus*.

Apparently distributed throughout the southern half of the United States, especially in the Southern States. Four species, 1 subspecies, and 2 varieties. Several of the best known members are *abditus* var. *etiolata* Wheeler of Texas, *mississippiensis* M. R. Smith of South Carolina, Mississippi, Louisiana, Illinois, and Oklahoma, and *pylartes* Wheeler of Texas, Louisiana, and Oklahoma. Species examined, *pylartes* Wheeler and *mississippiensis* M. R. Smith.

#### CAMPONOTUS, subgenus MYRMAPHAENUS Emery

*Camponotus* (*Myrmaphaenus*) Emery, 1920, Rev. de Zool. et de Bot. Africaines 8:237.

Subgenotype, *Camponotus leydi* Forel (by original designation).

Two species, *bruesi* Wheeler of Texas and *yogi* Wheeler of California. The male of each species is unknown. They will probably be found to have characters similar to those of the subgenus *Camponotus*.

#### CAMPONOTUS, subgenus MANNIELLA Wheeler

*Camponotus* (*Manniella*) Wheeler, 1921, Psyche 28: 19.

Subgenotype, *Camponotus sphaericus* Roger (by original designation).

A single species, *ulcerosus* Wheeler of Arizona, the male of which is unknown. The male will probably be found to have characters similar to those of the subgenus *Camponotus*.

#### CAMPONOTUS, subgenus MYRMOBRACHYS Forel

*Camponotus* (*Myrmobrachys*) Forel, 1912, Soc. Ent. de Belg. Mém. 20: 91.

Subgenotype, *Formica senex* F. Smith (by designation of Wheeler, 1913).

Length 4.5-5 mm.

One species and 1 subspecies, *planatus* Roger of Florida and Texas, and *mina zuni* Wheeler of Arizona. Characters similar to those of the subgenus *Camponotus*. Species examined, *planatus*.

## PARATRECHINA, subgenus PARATRECHINA Motschoulsky

*Paratrechina* Motschoulsky, 1863, Bul. Soc. Nat. Moscou. 36: 13.

Subgenotype, (*Paratrechina currens* Motschoulsky) = *Formica longicornis* Latreille (monobasic).

Length 2.6-3 mm. Head longer than broad. Antenna 13-segmented; scape extremely long and slender, approximately one and three-fourths times the length of the head; without suberect to erect hairs; funiculus subfiliform, the first segment not noticeably broadened, all segments distinctly longer than broad. Eye longer than broad, convex, not placed near base of mandible. Mandible moderately well developed, longer than broad, with one small apical tooth and several fine denticulae. Parapsidal sutures present but no Mayrian furrows. Wing with poorly developed stigma; a radial and a cubital cell but no discoidal cell. Legs extremely long and slender. Petiole moderately well developed, inclined, not so thick anteroposteriorly as with *Prenolepis*. Base of gaster with an impression for reception of petiole (Fig. 3, B). Genital appendages rather large and prominent. Stipes robust, with medianly directed apex. No cerci. Head, thorax, and gaster with fairly abundant, long, coarse, suberect to erect hairs; these very sparse or absent on femora and tibiae.

One introduced species, *longicornis* (Latreille), which is established in many of our larger towns and cities, especially those towns in States bordering the Gulf of Mexico and the Atlantic Ocean. This ant is apparently more widely distributed in Florida than in any other State. Males have been examined of this species.

## PARATRECHINA, subgenus NYLANDERIA Emery

*Prenolepis* (Nylanderia) Emery, 1906, Soc. Ent. de Belg. Ann. 50: 134.

*Paratrechina* (Nylanderia) Emery, 1925, In Wytsman, Genera Insectorum, Fasc. 183, p. 217.

Subgenotype, *Formica vividula* Nylander (by original designation).

Length 1.5-3 mm. Antenna 13-segmented; scape considerably less than one and three-fourths times length of head (usually one and one-half times or less); all segments of funiculus longer than broad, the first segment slightly broadened. Antennal fossa placed close to or touching posterior border of clypeus (Fig. 1, A). Scapes (usually) and tibiae with rather coarse, suberect to erect hairs, these less abundant than on head and thorax (the male of *bourbonica* Forel var. probably does not have any such hairs on the scapes and tibiae). Mandible well developed, usually with an apical tooth and some very small, indistinct teeth or else without teeth. No Mayrian furrows present but usually parapsidal sutures. Wing with distinct stigma; a radial and a cubital cell but no discoidal cell. Petiole well developed, inclined, often thickened anteroposteriorly. Base of gaster with an impression for reception of petiole (Fig. 3, B). No cerci. Genital appendages rather prominent. Stipes varying from rather robust, subtriangular, to more slender, digitiform.

Four species, 3 subspecies, and 3 varieties. Two of these are introduced, a variety of *bourbonica* Forel in Florida, and *fulva pubens* Forel in several green-

houses in at least the Eastern States. The native forms are most common in the eastern half of the United States and in the Southern States. Species examined, *parvula* (Mayr) and *fulva pubens* Forel.

#### PRENOLEPIS Mayr

*Prenolepis* Mayr, 1861, Die Europäischen Formiciden, p. 52.

Genotype, *Tapinoma nitens* Mayr (by designation of Bingham, 1903).

Length 2.5-4 mm. Antenna 13-segmented; scape long but not exceeding combined lengths of first 4 funicular segments; first funicular segment not noticeably wide, all segments longer than broad. Mandible rather well developed, longer than broad, indistinctly toothed except for apical tooth; mandible sometimes more or less concealed by clypeus. Eye longer than broad, strongly convex, not placed near base of mandible. Ocelli sometimes borne on a prominent protuberance above general surface of head. Parapsidal sutures present but no Mayrian furrows. Wing with well-developed stigma; a radial and a cubital cell but no discoidal cell. Petiole large, inclined, thick anteroposteriorly, with transverse superior border (Fig. 3, B). Base of gaster with an impression for reception of petiole (Fig. 3, B). Genital appendages large and prominent, but slender. Cerci present.

One species, *imparis* (Say) and 6 varieties. There are apparently one or more of these in all parts of the United States. Species examined, *imparis* (Say).

#### LASIUS, subgenus LASIUS Fabricius

*Lasius* Fabricius, 1804, Systema Piezatorum, p. 415.

Subgenotype, *Formica nigra* Linnaeus (by designation of Bingham, 1903).

Length, 2.5-3.5 mm. Antenna 13-segmented; scape as long as, or longer than, combined lengths of first 4 funicular segments; first funicular segment pyriform, distinctly wider than the following segment (Fig. 2, C). Mandible well developed, with 1 or 2 apical teeth, remainder of masticatory border toothless or with small, indistinct teeth. Eye almost subglobular but longer than broad, moderately convex to rather strongly convex, not placed near base of mandible. Maxillary palpus 6-segmented. Parapsidal sutures present but no Mayrian furrows. Wing with distinct stigma; a radial and a cubital cell; discoidal cell present or absent. Petiole erect, usually rather narrow anteroposteriorly, with superior border often very thin and emarginate. Base of gaster with an impression. Cerci present. Genital appendages prominent. Stipes varying from stout, subtriangular, to more slender, digitiform.

This subgenus contains 1 species, 3 subspecies, and 3 varieties, with representatives in all parts of the United States. Some of the best known forms are *brevicornis* Emery, *flavus nearcticus* Wheeler, and *niger* var. *americana* Emery. Species examined, *brevicornis*, *flavus nearcticus*, *niger* var. *americana*, and *niger* var. *neoniger* Emery.

## LASIUS, subgenus CHTHONOLASIUS Ruzsky

*Lasius* (*Chthonolasius*) Ruzsky, 1913, Arch. f. Naturgesch. Ser. A, Heft. 9, 79: 60.  
Subgenotype, *Formica flavus* Fabricius (by designation of Wheeler, 1916).

Length 2.6-4.5 mm. Characters similar to those of the subgenus *Lasius*.

Two species, 4 subspecies, and 1 variety. Representatives in all parts of the United States. The best known form is *umbratus mixtus* var. *aphidicola* (Walsh). Species examined, *umbratus minutus* Emery, *umbratus mixtus aphidicola*, *umbratus speculiventris* Emery, and *umbratus subumbratus* Viereck.

## LASIUS, subgenus ACANTHOMYOPS Mayr

*Acanthomyops* Mayr, 1862, Zool.-Bot. Gesell. Wien, Verh. 12: 699.  
Subgenotype, *Formica clavigera* Roger (by designation of Wheeler, 1911).

Length 2.6-5 mm. Characters similar to those of the subgenus *Lasius* except that the maxillary palpus is short and 3-segmented.

Nine species and 4 subspecies, one or more of which occur over all parts of the United States. The three best known forms are *claviger* (Roger), and *interjectus* Mayr of the eastern half of the country and *latipes* (Walsh), which is distributed over the entire Union. Species examined, *claviger*, *claviger subglaber* Emery, *interjectus*, *latipes*, and *plumopilosus* Buren.

## MYRMECOCYSTUS Wesmael

*Myrmecocystus* Wesmael, 1838, Brussels, Acad. Roy. des. Sci. de Belg. Bul. 5: 766.  
Subgenotype, *Myrmecocystus mexicanus* Wesmael (monobasic).

Length 3-7 mm. Antenna 13-segmented; scape very long and slender, approximately as long as the combined lengths of the first 6 or 7 funicular segments; funiculus slender, subfiliform; first funicular segment enlarged, usually distinctly pyriform. Eye moderately to strongly convex, generally placed at a considerable distance above base of mandible. Ocelli often very small. Maxillary palpus unusually long and slender, the fourth segment longer than the combined lengths of the fifth and sixth segments (Fig. 6, B). Mandible large, masticatory border with a prominent apical tooth; remainder of border toothless or with a few very small teeth. Parapsidal sutures present but no Mayrian furrows. Wing with a distinct stigma, which is often large; a radial and a cubital cell; discoidal cell present or absent. Legs long and slender. Petiole well developed, erect. Base of gaster not impressed. Cerci present. Genitalia prominent. Stipes subtriangular, usually not directed so strongly ventrad as with *Formica*.

Five species, 9 subspecies, and 8 varieties. Western and Southwestern with one or more representatives in the following States: California, Oklahoma, New Mexico, Arizona, Texas, Colorado, and Utah. The 2 most common species are *melliger* Forel and *mexicanus* Wesmael. There are 6 subspecies and 6 varieties

of *melliger* and 3 subspecies and 1 variety of *mexicanus*. According to Wheeler, *melliger* is most abundant at altitudes of about 300-1,500 meters, whereas *mexicanus* seems to find its optimum environment at about 2,000-3,000 meters. Species examined, *hammettensis* Cole, *melliger semirufus* Emery, *melliger semirufus kennedyi* Cole, and *mexicanus idahoensis* Cole.

FORMICA, subgenus PROFORMICA Ruzsky

*Formica* (*Proformica*) Ruzsky, 1903, Soc. Ent. Ross. Horae 36: 303.

Subgenotype, *Formica nasuta* Nylander (by designation of Wheeler, 1911).

Length 6-7.5 mm. Characters similar to those of the subgenus *Formica*.

*Proformica* contains 2 species, 1 subspecies, and 3 varieties. Representatives occur over most of the United States with the possible exception of the extreme southern section. The best known form is *neogagates* Emery. Species examined, *neogagates*.

FORMICA, subgenus NEOFORMICA Wheeler

*Formica* (*Neoformica*) Wheeler, 1913, Harvard Univ. Mus. Compar. Zool. Bul. 53: 388.

Subgenotype, *Formica pallidefulva* Latreille (by designation of Wheeler, 1913).

Length 7-10 mm. Characters similar to those of the subgenus *Formica*.

This subgenus contains 2 species, 4 subspecies, and 4 varieties. Representatives occur over most of the United States but the species are apparently most abundant in the eastern half of the country. The majority of the forms belong to the *pallidefulva* group, which includes the typical species and 7 variants. Species examined, *pallidefulva* Latreille, and *pallidefulva nitidiventris* Emery.

FORMICA, subgenus FORMICA Linnaeus

*Formica* Linnaeus, 1758, System. Naturae Ed. 10, p. 579.

Subgenotype, *Formica rufa* Linnaeus (by designation of Girard, 1879).

Length 5-10.5 mm. Antenna 13-segmented; antennal fossa contiguous with or in close proximity to posterior border of clypeus (Fig. 1, A); scape at least as long as combined lengths of first 4 funicular segments, all funicular segments longer than broad, the first funicular segment not appreciably broadened. Mandible longer than broad, with an apical tooth; masticatory border toothless or else usually with indistinct teeth. Clypeus usually weakly to strongly carinate. Ocelli small to large. Eye large and prominent, moderately to strongly convex, not placed near base of mandible. Fourth segment of maxillary palpus not exceeding combined lengths of fifth and sixth segments. Parapsidal sutures present but no Mayrian furrows. Wing with prominent stigma; a radial and a cubital cell; discoidal cell sometimes absent. Petiole erect, usually low, thick anteroposteriorly. Cerci present. Genital appendages large, their apices directed at an angle to longitudinal axis of body approaching a right angle (Fig. 3, C).

This subgenus is divided into 5 groups: *fusca* Linnaeus with 5 species, 2 subspecies, and 20 varieties (there are 6 variants of *cinerea* Mayr in addition to *fusca* and its 12 variants); *rufa* Linnaeus with 7 species, 5 subspecies, and 13 varieties; *microgyna* Wheeler with 9 species, 3 subspecies, and 8 varieties (in addition to *microgyna* there are 8 variants of it); *exsecta* Nylander with 2 species, 1 subspecies, and 2 varieties (*exsectoides* Forel and *ulkei* Emery are the two best known species); *sanguinea* Latreille with 9 species, 5 subspecies, and 3 varieties (there are 7 variants of *sanguinea*). Representatives of these five groups occur in all parts of the United States with the possible exception of the extreme southern section. The *rufa* group seems to be best represented in the western half of the United States, whereas those of the *exsecta* group are most common in the eastern half. Species examined, *fusca* var. *subaenescens* Emery, *fusca* var. *subsericea* Say, *lecontei* Kennedy and Dennis, *rufibarbis* var. *gnava* Buckley, *truncicola integroides haemorrhoidalis* Emery, *truncicola integra* Nylander, *difficilis* Emery, *habrogyna* Cole, *indianensis* Cole, *microgyna* Wheeler, *exsectoides* Forel, and *sanguinea aserva* Emery.

#### POLYERGUS Latreille

*Polyergus* Latreille, 1805, Histoire Naturelle, Générale et Particulière des Crustacés et de Insectes, vol. 13, p. 256.

Genotype, *Formica rufescens* Latreille (monobasic).

Length 6-7 mm. Antenna 13-segmented; scape approximately as long as combined lengths of first 3 funicular segments. Mandible narrow, elongate, pointed, somewhat sickle shaped; without masticatory border or teeth (Fig. 2, G). Clypeus strongly convex or subcarinate. Eye distinctly longer than broad, subreniform. Ocelli very small. Parapsidal sutures present but no Mayrian furrows. Wing with well-defined stigma; normally a radial and a cubital cell; discoidal cell usually present. Petiole emarginate. Cerci present. Genital appendages relatively small.

One species, 3 subspecies, and 4 varieties. *Polyergus lucidus* Mayr is the most common form in the extreme eastern section of the United States. Subspecies and varieties of *rufescens* Latreille occur in the Middle West and West, the subspecies *breviceps* Emery apparently being the most common form. Species examined, *rufescens breviceps*, *rufescens bicolor* Wasmann, and *lucidus* Mayr.

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## On a Species of *Macrostomum* (Turbellaria: Rhabdocoela) Found in Tanks of Exotic Fishes

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### I. Introduction

In 1882, von Graff described a new *Macrostomum* under the specific name *tuba*. The most salient character of this species is the tubular penis stylet with a bulbous tip (Fig. 13). It is to be noted that the animal came from a pond in the botanical garden in Munich and hence its endemicity may be questioned. In 1905, Luther published an account of the histology of the genus *Macrostomum*, based on three species, one of which was said to be *M. tuba*. The material of *M. tuba* consisted of three preserved specimens sent to Luther by Böhmig but the source of the specimens is not stated. Luther added many details to Graff's account of *M. tuba* but his figure and description of the penis stylet differ from those of Graff, showing the penis stylet with a simple oblique tip without bulbous enlargement (Fig. 15). If this is the correct shape of the stylet tip of Luther's specimens, then it would appear that those specimens could not have been *M. tuba*. However, Luther worked entirely from sections and probably the stylet tip had been cut away or lost in the sectioning process; Luther's figure (Fig. 15) certainly suggests some such mishap. It will be assumed in what follows that Luther actually had *M. tuba*.

In his 1913 monograph of the Rhabdocoelida, Graff gave a description of *M. tuba* which is simply a combination of his 1882 remarks with material added from Luther's work. Evidently Graff had had no fresh material of the species. He cited and figured as characters of the penis stylet of *M. tuba* both the bulbous tip of his own original description (Fig. 14) and the simple diagonal opening of Luther's description (Fig. 15). No species of *Macrostomum* can have two such differing penis stylets and hence the penis stylet of the original description must be taken as correct.

Between 1913 and 1930 there have been a number of records and descriptions in the literature of *Macrostomum* specimens identified as *tuba*. These are listed by Ferguson (1940) and will be referred to in detail later. Here I may say that probably none of them were actually *M. tuba* with the possible exception of the form used by Ruhl (1927) in regeneration experiments. Identification appears to have been based chiefly on the bulbous stylet tip of these forms without regard to other characters.

In 1930, Okugawa described as common in Japan a *Macrostomum* which he named *M. tuba gigas*, differing from *M. tuba* in size, body contour, and characters of the penis stylet. A more detailed description promised in the future apparently never appeared. Kepner and Stiff in 1932 published on a

rhabdocoel found in a pond near the University of Virginia which they considered to be an American representative of *M. tuba*. Their animal agrees with Graff's original description in body contour and general anatomy of the male apparatus; but differs in lacking lobulated ovaries and in having a penis stylet like that of Okugawa's form. They noted that the bulbous stylet tip is caused by a thickening of the wall, not by an expansion of the lumen as was the case with the original *M. tuba*; but this thickening had already been figured by Beklemishev (1927), Gieysztor (1930), and Okugawa (1930). In 1936, I identified as *M. tuba* a *Macrostomum* which I had found in abundance in tanks of exotic fishes in the greenhouse of the Department of Animal Behavior of the American Museum of Natural History, and which still exists in those tanks. This form appeared to me to agree satisfactorily with Graff's original description except for the penis stylet which in its much greater length and thickened tip resembled the figures of Beklemishev, Gieysztor, Okugawa, and Kepner and Stiff.

In 1939-1940, Ferguson published a monograph of the genus *Macrostomum* in which he described a number of new species and varieties, created a number of new names, and attempted to evaluate the species in the literature. Although this work is indispensable to future students of the genus and contains a valuable bibliography, the author unfortunately failed in many instances to conform to the international rules and stated the synonymy, apart from that copied from von Graff, in a very confusing manner, in footnotes and incidental remarks in the text. It appears, although this is not clearly stated, that Ferguson regards Kepner and Stiff's form as belonging to his new name, *M. bulbostylum*, and he also puts the forms called *M. tuba* by Beklemishev and Gieysztor under this species but *M. tuba gigas* Okugawa is left as a subspecies of *M. tuba*. Ferguson called attention to an important point which I had overlooked,<sup>1</sup> namely, that the bulbous stylet tip in Graff's 1882 description is caused by an expansion of the lumen (Fig. 14), whereas in all other figures of forms assigned to *M. tuba* except Ruhl's, it is caused by a thickening of the wall, without enlargement of the lumen (Fig. 9). If this character be taken to remove all these forms from *M. tuba*, then clearly Okugawa's animal cannot be a subspecies of *M. tuba*. Ferguson gives no grounds for the synonymy just stated and for reasons that will be stated later, I am unable to agree with his disposition of these forms.

In regard to *M. tuba*, Ferguson made the mistake of attributing to *M. tuba* a figure of the pharynx which he copied from Graff (1882) but which really pertains to *M. hystrix*. Graff gave only three figures of *M. tuba*: the male copulatory apparatus, the spermatozoon, and the adhesive papillae.

Ferguson dismisses my 1936 description with scant consideration as a "dubious species," and censures me for not having produced a more detailed

<sup>1</sup> Because of having overlooked this point, I failed in my 1936 article to understand correctly some remarks of Kepner and Stiff about the penis end; for this misunderstanding I apologize. I was also in error in that article in stating that Luther obtained his specimens from von Graff; he got them from Böhmig.

description and particularly for not having figured the excretory system, the stylet tip, and the spermatozoon. I did not see the excretory system and as this is not described for the original *M. tuba* or other specimens assigned to this species, it is not clear what aid it would have been to identification. As to the stylet tip, I stated that this in my animal was identical with the figures of Beklemishev and Okugawa and this should have been sufficient information. I was certainly at fault in not examining the sperm but as will appear later this would not have led to any certain conclusion either.

I have now restudied my animal and reached the same conclusion as previously, i.e., that my form differs from *M. tuba* (insofar as the original description goes) only in characters of the penis stylet, and that it is identical with the animal described as *M. tuba* by Beklemishev (1927) and as *M. tuba gigas* by Okugawa (1930). I also believe the *M. tuba* of Gieysztor's 1930 description (which I overlooked before) to be conspecific with my animal. If the characters of the penis stylet (greater length, thickened wall of the tip) are to be taken as of specific value, then it follows that neither I nor the other authors mentioned had *M. tuba* or a variety thereof, that Okugawa's subspecies must be raised to specific rank, and the name of the animal must be *M. gigas*.

The following is a redescription of my animal, which I now identify as *M. gigas*, based on renewed examination of many living individuals, normal and compressed, and of the sections of several animals prepared for my 1936 account.

## II. Description of *Macrostomum gigas* Okugawa 1932

The animal reaches a length of 3.5 mm., although most sexually mature worms are a little shorter than this; hence it is really large as compared with other *Macrostomums*, which are said by Ferguson to range from 0.8 to 2.5 mm. The body is of elongated oval form (Fig. 1), rounded at both ends, sides slightly outcurved, hence body widest through the middle third. The anterior end is often distinctly narrowed (more so than in Fig. 1) because of the indentations where the cilia cease (Fig. 2). The rear end is generally rounded in the extended moving animal but may be slightly expanded in especially large specimens as in Okugawa's figure; it is never, however, decidedly spatulate as in some *Macrostomum* species.

Most species of *Macrostomum* are said to be transparent or translucent but *M. gigas* is distinctly whitish to the naked eye; the digestive tract takes the color of recently ingested food. The ripe eggs in the oviduct and antrum are very opaque white under low magnification, gray with higher magnification. The purple color of the pharyngeal glands noted in my previous account (1936) was absent in the present specimens.

The anterior margin is devoid of cilia and provided with many (mostly 40 to 60 in mature specimens) stiff conical projections which appear to be tactile sensilla; they are evidently what Ferguson calls spines (Fig. 2). This spine-bearing margin is marked off from the adjacent ciliated epidermis by little

indentations, often quite marked even under low magnification. There are no such spines elsewhere on the body. Along the sides and rear end of the body there are a few scattered sensory hairs (Fig. 1), longer and more flexible than the spines. For the most part these occur singly, not in groups or tufts as described by Ferguson for a number of species. Occasionally a long sensory hair was seen to be accompanied by one or two shorter ones. The long sensory hairs are more numerous along the adhesive rear end than along the body sides (Fig. 3).

The posterior margin is provided with adhesive papillae (Fig. 3), which are retractile, hence visible only when the animal pauses and attaches. Such attachment involves only the papillate region which then spreads out in a fan-like manner (Fig. 3) and displays the papillae. The latter appear as short clear blebs somewhat irregular in length and shape (Fig. 3). The papillate region appears to be devoid of cilia, at least the cilia if present are shorter and less evident than elsewhere so that during attachment there is a clear demarcation between the papillate region and the regular ciliated epidermis (Fig. 3).

The epidermis is pierced between cells by bundles of rhabdites which as usual are much more numerous dorsally than ventrally. In my animal these bundles are about evenly distributed throughout the dorsal region, not more abundant along the body margins. The rhabdites are of clavate form (Fig. 5), about  $18-20\mu$  in length, up to ten per bundle, mostly six to eight. They appeared to be of about the same length throughout the body; especially long ones (thammites) connected by tracts to the brain occur in a small area of the anterior tip. Among discharged rhabdites there are to be seen some more attenuated at the narrower end than the majority, as in the right-hand rhabdite of Figure 5. These run to  $25\mu$  or longer. I found no rhabdites around the mouth as recorded for other species but there do seem to be some especial eosinophilous elements in a circle around the mouth.

The eyes of my animal, situated immediately in front of the pharynx and immediately behind the main nervous mass, appear in compressed specimens as a pair of reniform black masses each curved around a rounded clear body. The latter is usually called a lens in taxonomic descriptions of *Macrostomum*, and appears to be evident in low-power examination of the eye in all species, hence of no taxonomic value. This is not really a lens (extra-retinal refractive body) but a part of the retinal cell. As is well known, the eye of *Macrostomum* consists of a single retinal cell inverted into a pigment cup. The retinal cell has the usual parts known to be characteristic of the turbellarian eye since the classical work of Hesse (1896), i.e., a rod or striated border, a clear region ("lens" of various authors), and a proximal part containing the nucleus and continuing by a nerve fiber into the adjacent brain. The best eye section on my slides is shown in figure 4. My findings are similar to those of Kepner and Stiff although I see no grounds for the terminology developed by Kepner for the regions of the retinal cell.

No attempt was made to work out the nervous system in detail but incidental observations indicate close similarity with Luther's figure (1905, text fig. 3)

of the nervous system of *M. tuba*. A sketchy representation of my findings has been added to figure 1. The main nervous center or brain appears as a thick band passing in front of the eyes; this continues backward on each side as a ventral nerve cord which encircles the viscera of the worm. The posterior part of this continuous cord, passing behind the male apparatus, was mistaken by Okugawa for an excretory vessel. From the brain a network of nerve strands can be seen permeating the precerebral part of the anterior end and especially supplying the anterior margin; many fine branches also pass from the rear part of the nerve cord into the adhesive posterior end. There is also a nerve ring around the pharynx connected on each side with the ventral cord by a connective; the exact manner of junction of the pharyngeal ring with the brain was not clearly ascertained. It seems probable that the main features of the nervous system—the encircling cord and the pharyngeal ring—are common throughout the genus.

The digestive system offers nothing of specific value. The mouth slit occupies about two-thirds the length of the pharynx. The pharynx is an oval muscular organ connected to the intestine by a brief narrowed esophagus. Mouth and pharynx are capable of great distension. In sections the pharynx is seen to be lined by a tall ciliated epithelium and as already noted there is a ring of elongated slightly eosinophilous structures in its wall near the mouth. The intestine is an elongated sac, tapering to a point posteriorly just in front of the male apparatus. It has slightly wavy walls composed of a tall bulbous epithelium, packed in most of my sections with food balls resembling those seen in the intestinal epithelium of planarians; their presence suggests that digestion in *Macrostomum* must be largely intracellular.

Despite repeated efforts I was totally unable to see any trace of the excretory system. Aqueous eosin as recommended by Ferguson proved of no value for rendering the excretory vessels visible in my species. Azur II was not available. As already mentioned what Okogawa regarded as a transverse excretory vessel in the rear part of the animal is in reality the nerve cord. I was myself deceived by this for a time and probably the same mistake has been made with other species of the genus.

The reproductive system conforms to the general plan for the genus. The testes are elongated, slightly lobed, cylindrical bodies alongside the anterior part of the intestine (Fig. 1). They are rather transparent and rendered visible chiefly by the sperm accumulations in their lumen. From the rear end of each testis a sperm duct proceeds backwards alongside the intestine behind the rear end of which the two ducts enter an expansible thin-walled sac of changeable shape. This is called false seminal vesicle in the literature but since it functions as a genuine storage sac for the sperm, the name is not a happy one and spermiducal vesicle is suggested instead. From the rear wall of this (Fig. 8), a narrowed tube leads into the seminal vesicle, of cylindrical form, thicker-walled and of more definite shape but smaller than the spermiducal vesicle. The seminal vesicle is directed anteriorly and leads into the granule vesicle, also directed anteriorly. The granule vesicle is a firm body of fusiform shape,

whose proximal part is surrounded by eosinophilous granule glands, containing coarse eosinophilous granules, which are discharged into the granule vesicle by several conduits (Fig. 8). The distal end of the granule vesicle narrows to a curved tube which incloses the proximal end of the penis stylet. The latter is a long curved tube of hard material (usually called chitin but not proved to be this substance) which is directed backwards and tapers slightly to its tip. This tip lies at the male genital pore and is of bulbous shape because of a ring-like thickening of the wall (Fig. 9). The penis stylet is some three or four times the length of the granule vesicle (not counting the arched neck of the latter). As the stylet is curved, often markedly so, it is difficult to get an exact measurement of its length. The length is certainly subject to wide variation but in most specimens seems to be 400 to 500 $\mu$ .

The fresh spermatozoon (Fig. 6) is an elongated filament tapering at one end into a flagellum ("feeler" of Ferguson), kept in constant undulation, and having for its other end a long filamentous tail always writhing and twisting about. There is no obvious enlarged "body," but the part bearing the flagellum evidently corresponds to the body since this remains quiescent, apparently adhering to the substratum, while flagellum and tail are in constant motion. Sections show that this body part contains the nucleus. At the junction of body and tail there are two bristles or setae but I was able to see these only with the greatest difficulty. Because of the constant writhing of the fresh sperm, it is impossible to get an accurate measure of their length but they appear to be 40 to 50 $\mu$  long. After a short exposure to water, the body of the sperm swells to a globular shape (Fig. 7) and the tail shortens greatly. The sperm then resembles Graff's 1882 figure of the sperm of *M. tuba* and also other figures of *Macrostomum* sperm in the literature. As one cannot know whether or not these figures are based on fresh sperm or sperm swollen with water, their taxonomic worth is dubious. Gieksztor also found that the sperm of the animal she called *M. tuba* is filamentous when fresh and comes to resemble Graff's figure only after exposure to water.

The ovaries (Fig. 1) are situated behind the testes, one on each side, slightly shorter than the latter. They are so transparent as to be seen with difficulty in the living animal but become more visible after staining with aqueous eosin. They are highly lobulated, consisting of many small lobes attached to a central region from which a broad oviduct, often distended with several ripe ovocytes, proceeds posteriorly. In the available sections I was not able to see any transitional stages between the very young ovocytes in the lobes of the ovary and the ripe ovocytes. An oviducal wall around the ripe ovocytes is detectable with difficulty in sections. I was unable to trace the oviducts into the female antrum or to determine whether they unite to a common oviduct before entering the antrum. However, one of my sections shows a ripe ovocyte in process of passing into the antrum through an opening in the anterior wall of the latter and one may presume that the ovocyte is coming from a common oviduct especially as this latter structure appears to be general throughout the genus.



The female antrum is a large rounded chamber ventral to the rear end of the intestine. Its wall consists of a cuboidal epithelium which when the antrum contains an egg become so stretched that cell boundaries are no longer detectable in some places (Fig. 10). The antrum opens ventrally by the female genital pore and is surrounded by a great halo of eosinophilous glands which open through the tall epithelium bounding the genital pore (Fig. 10). These glands probably secrete some adhesive material causing the egg shells to stick to objects. Such cement glands in connection with the female apparatus are of common occurrence throughout the Turbellaria.

As they proceed towards the antrum the ovocytes begin to show a peripheral layer of spherules and these form a definite surface layer of the ovocyte in the antrum (Fig. 10). These spherules presumably fuse and alter to form the egg shell. A mitotic figure is evident in the ovocyte in the antrum (Fig. 10) and appears to be the figure for one of the maturation divisions. In the best figure found on my sections, three chromosomes are evident (Fig. 10) so that apparently reduction had already occurred and the diploid chromosome number is six, as appears to be the rule throughout the genus. The material was not favorable for determining the shape of the chromosomes but they seemed to be V-like.

Numerous sperm are evident in the antrum in the sections so that presumably fertilization takes place in this chamber or in the oviducts.

My animal breeds freely in small dishes. Pairs in copulation were often observed but separated as soon as touched so that the relations of parts in copulation could not be ascertained. The copulatory attitude is the same as depicted by Ferguson (1939, p. 8). Presumably the penis stylet is inserted in the female genital pore of the partner. Ferguson claims that the fertilization is one-sided although mutual fertilization is the rule among the Turbellaria. A specimen examined immediately after copulation showed both spermiducal and seminal vesicles emptied of sperm and scattered active sperm in the granule vesicle and penis stylet.

The eggs are found in large numbers adhering to debris on the sides and bottom of the culture dish. They are spherical brown objects each containing a single embryo. Development is rapid and at room temperature the eggs hatch in probably not much more than a week. The complete little worm is seen curved inside the egg shell making movements of escape. The actual hatching was not witnessed but the empty shells show a neat round hole (Fig. 11). The young worms are transparent, of clavate shape, with disproportionately large eyes and brain ganglia (Fig. 12). They grow rapidly to sexual maturity and begin to show sperm and ripe ovocytes when not much more than 2 mm. long.

The animal is easily cultured in finger bowls in the laboratory and may be fed crushed *Daphnia*, chopped mealworms, or naid annelids such as *Dero* which in turn are easily grown in lettuce culture (Hyman, 1941). Although *Dero* is many times larger than the *Macrostomum*, the latter attacks the

annelid without hesitation and with widely distended mouth quickly swallows a large piece of the *Dero*. During the attack, the *Macrostomum* attaches to the substratum by its adhesive papillae but does not let go its prey even when torn loose from its hold by the writhings of the annelid. After being gorged with food, *Macrostomum* retires under a piece of debris and remains quiescent in a contracted almost circular shape. The animals are negative to light, positive to contact. *Macrostomum gigas* will also flourish in hydra cultures, feeding on the excess *Daphnia* or other food supplied to the hydras.

The present species has been found only in tanks of exotic fishes in the American Museum of Natural History and is evidently not endemic to the United States.

### III. Synonymy and Comparisons

There is a confusion in the literature between *M. tuba*, *M. gigas*, and *M. bulbostylum*. Because of the lack of details in many of the available descriptions this confusion cannot be definitely cleared at present and the following is presented merely as a preliminary attempt at evaluation of these forms.

#### MACROSTOMUM TUBA (Graff), 1882

Syn. *Macrostoma tuba* Graff, 1882.

*Macrostoma tuba* Graff, Luther, 1905

*Macrostomum tuba* (Graff), Graff, 1913

*Macrostomum tuba* (?) Ruhl, 1927

Characters from the original description: 2.5 mm. long, broadest in the anterior third, both ends rounded, hyaline, anterior margin with sensory spines, posterior margin with retractile adhesive papillae, rhabdites clavate,  $15\mu$  long, eyes with evident "lens," shaped as in *M. hystrix* (i.e., somewhat hemispherical), male copulatory apparatus (reproduced in my figure 13) with spermiducal vesicle, fusiform seminal vesicle, retort-shaped granule vesicle provided proximally with granule glands, tubular penis stylet, not much longer than granule vesicle, tapering to bulbous tip caused by expansion of the lumen (Fig. 14), sperm (probably swollen with water) with oval body, three setae, slender tail. Locality, pond in botanical garden, Munich. Added from Luther's description: sensory hairs in groups, rhabdites more numerous along body margins where also longer ( $16-20\mu$ ) than dorsally ( $8-13\mu$ ), long slender rhabdites (?) around mouth, sperm filamentous, ovaries highly lobulated, broad oviducts unite to small common oviduct.

It is my opinion that *M. tuba* has not been seen again since the original description. Of the many records of this species in the literature, that of Ruhl, 1927, is the only one that might be *M. tuba* with any probability. Ruhl figures the entire animal and the penis stylet. The former resembles the original description in being widest through the anterior third but differs in that the rear end is decidedly spatulate. The penis stylet is also similar to Graff's original figure but it cannot be decided from Ruhl's drawing whether the bulbous end is caused by a widening of the lumen or a thickening of the wall.

Of the other records of *M. tuba*, the following are mere locality records so that the identification may be doubted: Plotnikov, 1906, region of Bologoje, province of Novgorod, Russia; Steinböck, 1926, flowing water in Steirmark, near Graz, Austria; Valkanov, 1926, Bulgaria; and Vialli, 1927, Cremona, Italy. Fulinski (1915) reported finding *M. tuba* in Poland, giving as the only description the statement that the penis stylet resembles the drawing of Luther, having a slightly expanded tip. This is a most bewildering remark, since the trouble with Luther's drawing (reproduced here as figure 15) is that it does *not* show an expanded tip. (Perhaps Fulinski referred to the other penis stylet figured by Luther and doubtfully attributed by him to *M. tuba*). Sibriakova (1929) doubtfully identified as *M. tuba* specimens from the Angara River, Russia, but her figure of the penis stylet and granule vesicle shows that the animal could not have been either *tuba* or *gigas*. In their report of *M. tuba* from Poland, Fulinski and Szynal (1932) mention only that tufts of tactile hairs are limited to the anterior body third. This excludes *M. gigas* and is of doubtful applicability to *M. tuba* as Luther implies an even distribution of sensory tufts in the latter.

#### MACROSTOMUM GIGAS Okugawa 1930

Syn. *Macrostomum tuba* (Graff), Beklemishev, 1927  
*Macrostomum tuba* (Graff), Gieysztor, 1930  
*Macrostomum tuba gigas* Okugawa, 1930  
*Macrostomum tubum* (Graff), Hyman, 1936  
(Not *Macrostoma tuba* Graff, 1882)

Characters from the original figures and description: 3.5 mm. long, anterior end somewhat narrowed, body widest through middle third, anterior margin with sensory spines, posterior end slightly expanded, with adhesive papillae, eyes reniform with distinct "lens," ovaries lobulated, penis stylet a long curved tube, terminating in a bulbous inflation caused by thickened wall, granule vesicle fusiform, penis stylet about three times the length of the granule vesicle. Added from present description: anterior margin bearing sensory spines devoid of cilia, posterior end expanded only in largest specimens, mostly rounded, adhesive papillae retractile, visible only during attachment, sensory hairs along sides and posterior margin mostly single, rhabdites clavate, mostly 18-20 $\mu$  long, bundles evenly distributed throughout dorsal surface and body margins, everywhere of about equal length, ovaries of many small lobes attached to central strand which continues as broad oviduct, male apparatus with expansible spermiducal and smaller tubular seminal vesicle (these two vesicles not shown as distinct in Okugawa's drawing), sperm filamentous, about 50 $\mu$  long, with two setae, alters greatly after short exposure to water. Locality, lakes, ponds, and rice fields in Japan, imported into the United States with exotic fishes; also if above synonymy is correct, common in eastern Europe, and probably a widespread Eurasian species.

It is evident that *M. tuba* and *M. gigas* have very similar characters, differing only in size, body contour, shape of the eyes, length of the penis stylet, shape of the granule vesicle, construction of the bulbous tip of the stylet,

possibly in shape of sperm. It might well be questioned whether these differences are of specific rank, but on the basis of the available information, it seems best to so consider them at present. To prove that they are variations of one species it would be necessary to show that intermediate forms exists.

I regard the *M. tuba* of Beklemishev's 1927 description to be really *M. gigas* because of its large size (4 mm. long or even more), and because the penis stylet in length, shape, and bulbous tip is identical with that of my specimens. I also consider the *M. tuba* of Gieysztor's 1930 description to be *M. gigas* because of the whole male apparatus as figured by her is indistinguishable from that of my specimens and because she found the sperm to be filamentous and to alter on exposure to water. Other points mentioned by these two authors fit either *tuba* or *gigas*.

#### MACROSTOMUM BULBOSTYLUM Ferguson 1939

Syn.? *Macrostomum tuba* (Graff), Kepner and Stiff, 1932  
(Not *Macrostoma tuba* Graff, 1882)

Characters from the original description and figures: 2.5 mm. long, anterior end rounded without sensory spines, posterior end spatulate without adhesive papillae, rhabdites shown as oxete in one figure, clavate in another, rhabdites more numerous along body ends than elsewhere, sensory hairs in tufts, occurring along whole margin, penis stylet straight, with bulbous tip due to thickened wall, ovaries compact, indented, spermatozoon like Graff's 1882 figure but has two setae instead of three. Locality, ponds, streams, lakes, springs, Virginia, Tennessee.

On paper, *M. bulbostylum* appears to be quite different from *M. tuba* and *M. gigas*. However, many of the stated differences could not be verified on examination of the paratypes deposited by Ferguson in the U. S. National Museum and kindly lent for examination by that institution. This material consists of six whole mounts and eleven sets of serial sections. I find on study of the whole mounts that the rhabdites are clavate, the ovaries are lobulated, the penis stylet is curved in all six specimens, and the whole male apparatus (not figured or well described by Ferguson) is identical with that of my specimens. As to the rhabdites Ferguson's account and figures are confusing and contradictory. In his figure 22, the rhabdites are shown as oxete (although this is not mentioned in the text) and in his figure 23, they are shown as clavate with a little tip to the broad end. I saw no oxete rhabdites on the paratypes and nothing but the simple clavate rhabdites such as those of my animal. The ovaries on the whole mounts and sections appeared to me to be lobulated and not to differ from those of my animal. I could see no difference in length, shape, or bulbous tip of the penis stylet from those of my specimens and others in the literature which I consider to be *M. gigas*. In short there remain as characters of *M. bulbostylum* which apparently differentiate it from *M. gigas* only the following: rhabdites are more numerous on the two ends than elsewhere, the sensory hairs occur in tufts, the anterior margin lacks sensory spines, and the posterior margin lacks adhesive papillae. The first was

verified on the paratypes; the last three could not be checked as living material is necessary for their study. The sperm figured by Ferguson resembles that of my animal after exposure to water and has no diagnostic value until the conditions under which it was drawn are known. Many of the points mentioned by Ferguson are either too trivial for specific diagnosis or else are common to many if not all species of the genus (i.e., the parts of the retinal cell).

Ferguson regards the animal described by Kepner and Stiff as belonging to *M. bulbostylum*. There are some discrepancies between the text and the figures in Kepner and Stiff's article. In a letter Dr. Kepner has informed me that the figures are to be taken as correct. It would then appear that their animal differs from Ferguson's description in lacking a spatulate rear and from Ferguson's paratypes in having non-lobulated ovaries. However, it probably is the same form as Ferguson's *M. bulbostylum*, allowing for inaccuracies and discrepancies in the descriptions. Ferguson also considers the forms of Beklemishev and Gieysztor to be *M. bulbostylum*. This is impossible since Beklemishev's animal had adhesive papillae<sup>2</sup> and Gieysztor's had filamentous sperm, also lobulated ovaries (denied by Ferguson for *M. bulbostylum*).

If the characters of the male copulatory apparatus, especially of the penis stylet, are to be regarded as the most important diagnostic characters for the species of *Macrostomum*, then there is no difference in this apparatus between *M. bulbostylum* and *M. gigas* (according to my examination of the paratypes of the former) and the former should probably be considered an American subspecies of *M. gigas*.

#### IV. Summary

The species of *Macrostomum* which often appears in the literature under the name of *M. tuba* (Graff) 1882 is considered to be identical with *M. tuba gigas* Okugawa 1930; this is raised to specific rank. Specimens now believed to be *M. gigas*, formerly attributed to *M. tuba*, occur in tanks of exotic fishes in the American Museum of Natural History and are used as a basis for a detailed description of *M. gigas*. *M. bulbostylum* Ferguson 1939, confused by Ferguson with *M. gigas*, is considered to be a subspecies of the latter, pending less conflicting information as to its characters.

#### LABELS OF ALL FIGURES

1, sensory spines; 2, nervous system; 3, mouth; 4, pharynx; 5, pharyngeal ring of nervous system; 6, testis; 7, intestine; 8, ovary; 9, oviduct; 10, ripe eggs in oviduct; 11, sperm duct; 12, ripe egg in female antrum; 13, spermiducal vesicle; 14, seminal vesicle; 15, granule vesicle; 16, penis stylet; 17, pigment cup of eye; 18, rod border of retinal cell; 19, retinal cell; 20, nucleus of retinal cell; 21, brain; 22, granule gland cells attached to granule vesicle; 23, peripheral layer of spherules of egg composed of shell material; 24, cement glands; 25, female genital pore.

<sup>2</sup> I am greatly indebted to Miss Francesca La Monte of the department of ichthyology of the museum for translating for me the original Russian text of the articles of Beklemishev and Sibirakova.

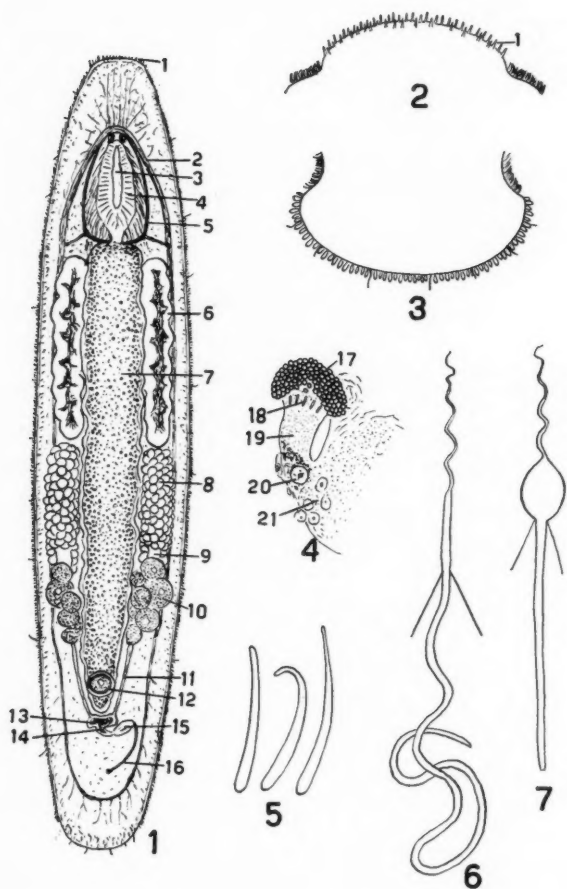


Fig. 1. *Macrostomum gigas* from life, shape carefully drawn from extended, freely moving animals, details added from study of compressed live specimens. Fig. 2. Anterior margin of *M. gigas*, showing sensory spines, and lateral indentations where cilia cease. Fig. 3. Posterior end of *M. gigas* during attachment showing protruded adhesive papillae, visible only at this time. Fig. 4. Section of the eye of *M. gigas*. Fig. 5. Rhabdites of *M. gigas*. Fig. 6. The fresh normal spermatozoon of *M. gigas*. Fig. 7. The spermatozoon after swelling from exposure to water.

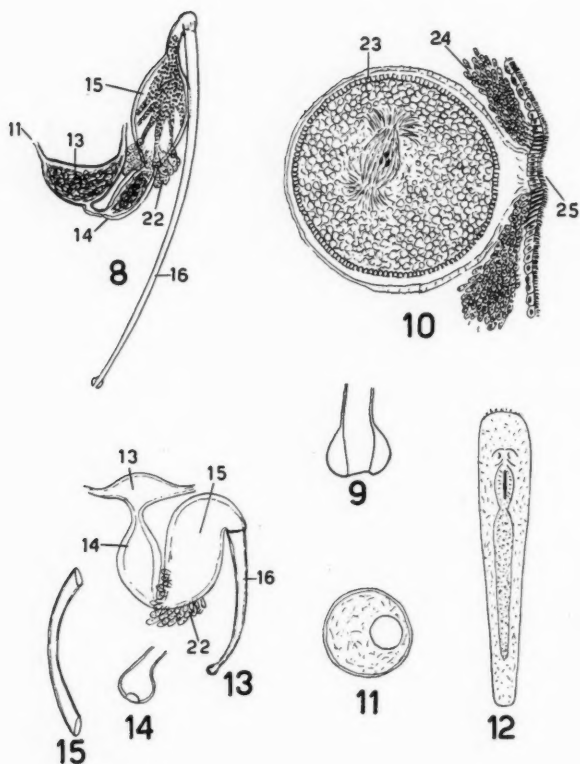


Fig. 8. The male copulatory apparatus of *M. gigas*. Fig. 9. The tip of the penis stylet enlarged to show bulbous thickening of the wall. Fig. 10. Sagittal section through the female antrum and genital pore of *M. gigas*, showing an egg in mitosis in the antrum, and the cement glands opening around the genital pore. Fig. 11. Hatched egg of *M. gigas*, showing hole through which young worm escapes. Fig. 12. Recently hatched young worm. Fig. 13. The copulatory apparatus of *M. tuba* traced from the original figure of von Graff 1882. Fig. 14. The penis tip from Fig. 13, enlarged. Fig. 15. The end of the penis stylet of *M. tuba* according to Luther, 1905; drawn from sections and probably lacking the true tip.



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AMERICAN MUSEUM OF NATURAL HISTORY,  
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## A Second Survey of the Anostracan Phyllopods in Northeastern Ohio<sup>1</sup>

Ralph W. Dexter

A survey of temporal vernal pools and ponds in Portage and Summit Counties was made by Dexter and Sheary (1943) during the late winter and early spring of 1941, after two years of preliminary collecting, to determine the seasonal and geographic distribution of anostracan phyllopods (fairy shrimps). The writer, during March and April of 1942, repeated observations on all but two of the ninety-seven pools previously studied. Two of them are now situated within the Ravenna Ordnance Plant and were not available. In addition, ten new ponds in Portage and Summit Counties were included in the second summary. Two ponds near Canton in Stark County from which collections had been made in 1940 and 1941 were revisited and ten additional ones in this County examined.

Eleven pools which were found to contain *Eubbranchipus vernalis* (Verrill) in 1941, also had populations of this fairy shrimp in 1942. One had a much larger population than during 1941, while four were found to have a smaller population. One of these stations, near Canton, was found to contain also small numbers of a second species, *Pristicephalus bundyi* (Forbes), the first record of this species known for Ohio. This species was not observed in the collections from this pond in 1940 and 1941 although it may have been present and remained unnoticed among *Eubbranchipus vernalis* which it closely resembles. *P. bundyi* has been previously reported from Massachusetts, New York, Michigan, Illinois, Wisconsin, Quebec, Ontario, Alberta, Yukon, and Alaska.

Four pools which contained *E. vernalis* in 1941 did not have any fairy shrimps during the season of 1942. In all but one case they were not particularly abundant the previous year, but this one is known to have had abundant fairy shrimps for a number of consecutive years. Three other pools which had none the first year, were found to have good sized populations of *E. vernalis* during the spring of 1942. Fairy shrimps returned to a pond from which they were collected in 1940 but were not present in 1941. This last season they were as numerous as in 1940.

Of the twenty new ponds visited, eight contained *E. vernalis*. Two of these had a very small sample—two specimens only being collected from each.

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<sup>1</sup> Read before the section on Zoology of the Ohio Academy of Science April 17, 1942, at Denison University, Granville, Ohio.

Seventy-eight pools lacked fairy shrimps during the two consecutive years, and twelve new stations did not have them during the second survey.

For the second year, then, a total of twenty-three temporary vernal pools out of a total of one hundred seventeen (19.7%) contained populations of anostracan phyllopods, all of them having *E. vernalis*, and one pool containing in addition a small number of *Pristicephalus bundyi*. In most cases it has been the experience of collectors to find but a single species in any one pool. Dexter and Ferguson (1943) never found *Eubranchipus vernalis* and *E. serratus* together in pools they studied in east central Illinois. Creaser (1930) found that two other anostracan phyllopods, *Streptocephalus sealii* and *S. texanus*, had never been found together in the same pool although their ranges overlap. Holmes (1910), on the other hand, reported that *Eubranchipus ornatus* and *Pristicephalus bundyi* (formerly *E. bundyi*) had been occasionally found in the same pond, and Ferguson (1939) collected *E. vernalis* and *P. bundyi* together in two pools although they were usually found separate. Mathias (1937) quoted several records where various phyllopods were found living in the same pond, but in each case a notostracan was found with an anostracan, and no case of two species of anostracans collected together was cited. The writer has in a number of instances found ostracodan crustacea which are closely related to phyllopods together with Anostraca. During the early collections of the second survey, thirteen ponds were found inhabited by Ostracoda, one of which also contained the fairy shrimp *E. vernalis*. Three of those with ostracods are known to have had *E. vernalis* in 1941 but not in 1942. Ostracoda were absent from one pond from which they had been collected in 1941. Anostraca, however, were present both years in this pond. During the latter part of the fairy shrimp season, late in April, three ponds which were revisited for specimens of *E. vernalis* were also found to be inhabited at this time with Ostracoda. Probably many other ponds which did not yield ostracodan crustacea in the early spring did contain them in the late spring. Apparently these hatch later than the anostracan phyllopods, at least in the ponds studied here.

The first collections of fairy shrimps in the season of 1942 was made on March 15. At that time the specimens were about equal in development to those collected from the same pond on March 6 of the preceding year. The first adults were collected on March 26, 1942, while in 1941 adults were first observed in that pond on March 20. Females with eggs were collected first on March 29, during the second year, and on March 22, during the first year. Specimens were collected throughout April but could not be found on May 10, 1942. In general, the fairy shrimp season of 1942 was about one week later than in 1941 for each particular pond.

As was observed for *Eubranchipus serratus* in Illinois (Dexter and Ferguson, 1943) great variation was found in the color of *E. vernalis* from different pools although all specimens from any one pool were quite uniform and sometimes characteristic in color. Specimens from many pools were orange-pink,

from others light orange, and from two pools they were colorless. From eight, the females were bluish-gray in color while the males were light green. These latter individuals were larger than the more characteristic orange and orange-pink populations. Pearse (1913) also observed sexual dimorphism in regard to coloring, that of *E. serratus* (published under the synonym of *E. dadayi*).

Mathias (1937) was able to distinguish two races of *E. vernalis* and of other fairy shrimps on the basis of size. These were found in separate pools, often in neighboring ponds, but never together. It appeared at first that possibly two separate races were represented in the collections from northeastern Ohio. The typical orange and orange-pink populations averaged 13.1 mm. in length, measured to the end of the abdomen, while the larger "race" averaged 21.6 in length.

It was discovered during return visits to three of the ponds which had the typical orange-pink populations that late in the fairy shrimp season the females were larger and at this time were bluish-gray while the males were light green. These were not, however, quite as large as those of similar colors collected elsewhere earlier in the season. Those which had changed from orange-pink to bluish-gray and green averaged 16 mm. in length. It is known that anostracan phyllopods change color as they get older (Dexter and Ferguson, 1943), and it may possibly be that any population could under certain conditions, mature into the bluish-gray females and greenish males of the larger "race." There is no evidence known by which one may distinguish the so-called "races" genetically. On the same day individuals of varying sizes can be collected in different ponds, although in any one they are rather uniform until the second brood hatches, as has been reported earlier (*ibid*).

These observations would indicate that in spite of size and color differences for the populations studied by the writer, there is no substantial evidence for more than a single race. Differences in size and color seem to be due to local variations, and are most evident during the early stages of development and among the first adults to mature. Also, many differences are the result of the time of seasonal appearance. The adults during the latter part of the fairy shrimp season are much more uniform in regard to size and color.

In most instances anostracan phyllopods can be easily detected when present. Ordinarily the populations are large and the fairy shrimps swim actively about in the open water and can be readily seen. In some few instances the number of individuals was found to be small, and intensive collecting was required to find them. This is most apt to be true late in the shrimp season when they become negatively phototropic and begin to die off with the rising water temperature. Also, at this time, their activity seems to vary from day to day.

Acknowledgment is made to Dr. M. S. Ferguson for a critical reading of the manuscript.

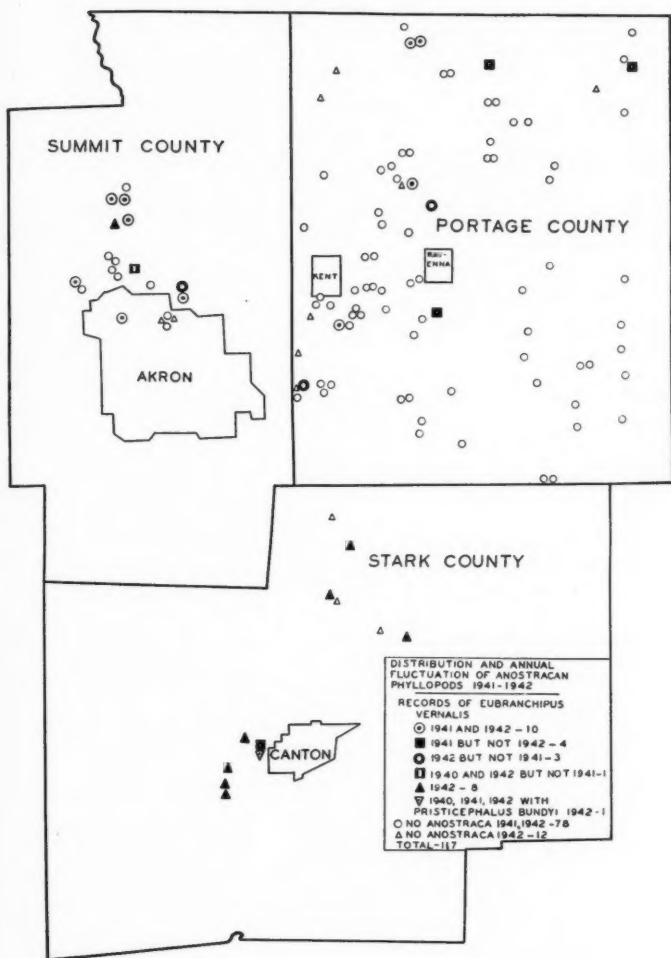


Fig. 1. Results of second annual survey of anostracan phylloped distribution.

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## The Mating of the Landsnail *Haplotrema concavum* (Say)

Glenn R. Webb

### Introduction

*Haplotrema (Geomene) concavum* (Say), the most widely distributed carnivorous landsnail of North America, is the only representative of its family east of the Rocky Mountains (Baker 1939, p. 91). The data presented below are the result of observations made on three pairs of mating specimens. All of the snails used in the study (nearly two dozen) were collected in Marion County, Indiana. Some of the specimens were obtained at Wollen's Garden NE of Millersville, and the remainder from a wood-land (Loc. 2x) located about the Pennsylvania Railroad Bridge over the Dietrich-Kline Ditch west of Mitthoefer Road.

The specimens were kept both in group and solitary confinement cages. The group method allowed the animals to mate at will and necessitated frequent inspections to witness the animals in the act. The solitary confinement method permitted individuals to be paired off for possible matings at the investigator's convenience. While post-midnight vigils are thus minimized, the added work in culturing the snails individually must be considered; my limited experience indicates neither method is superior to the other—both having special advantages and disadvantages. The maintenance of the animals was much simplified by having available as food for *Haplotrema* ample quantities of young of the European Brown Snail, *Helix (Cryptomphalus) aspersa* Müller. Perhaps because of improper culture conditions, I have found it difficult to keep *concavum* specimens active in confinement.

### Mating-procedure

Mating commences when one specimen mounts the shell of a sexually active companion and orientates itself so that its genital pore side (right side) is above that of the other snail. The upper animal then crawls forward on the last whorl toward the aperture of the lower animal; when it reaches the aperture rim, its head and neck are thrust downward while the lower animal arches its head upward. The result of these respective movements is that the head of the lower snail contacts the genital pore side of the upper and similarly the upper snail contacts that of the lower. The animals then commence gnawing at each other's foreparts. This continues for several minutes and during this time the sex organs are extruded. Because the heads and necks of the two animals are closely appressed and somewhat entwined during the gnawing procedure, the genital pore of each is not visible and the extruding organs can be seen only after they are well everted. This is accompanied by the



turgescence and eversion of the penis and atrium—the mass of the extruding parts separating the appressed foreparts of the animals and thus becoming visible. At about this time each snail's penis is inserted into the other's vagina and shortly the animals cease to gnaw at each other. Non-reciprocity has not been demonstrated in this species.

The proximity of the specimens and the mass of the lobular structures of the everted atrium prohibit observation of the inception of coitus. The appearance and relationship of the organs, however, is clearly interpretable upon the dissection of the mating-anatomies of copulating animals. In these the sex organs are as follows (see Figs. 1-5):

*Penis.*—The fully exerted penis appears as a strongly club-shaped, densely papillose body. The papillae are smaller at the penis-tip of the fully or almost fully everted organ. The basal portion of the penis is stalk-like, about one-

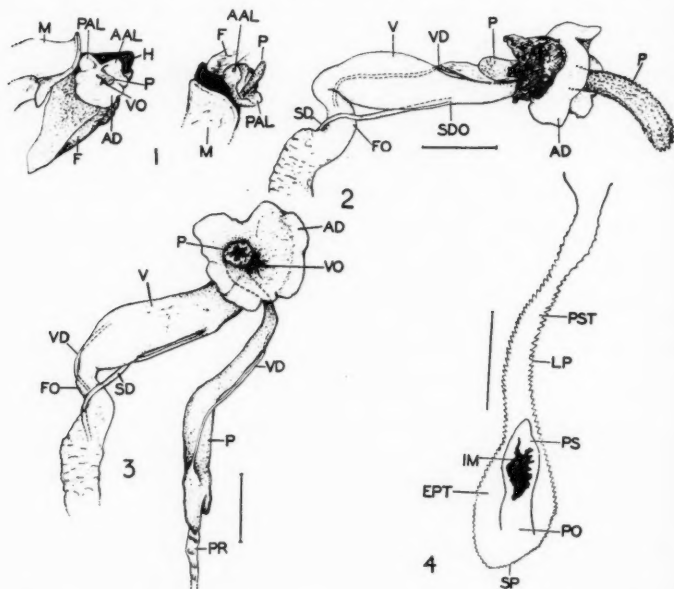


Fig. 1. Lateral and dorsal views of two mating-anatomies (greatly enlarged).

Fig. 2. The dissected sex organs of a mating-anatomy. The penis is incompletely everted.

Fig. 3. Sex-organs of the mate-animal of Fig. 2. Note the nearly complete retraction of the penis.

Fig. 4. The outline of an almost completely everted penis.

third the width of the apical parts, and about 7 mm. long (measurements based on material killed in boiling water). The entire penis is about 11 mm. long, the rather abrupt apical expansion commencing well past the middle. The penis may be even longer as the apical part (which ordinarily receives the vas deferens and penis retractor) is unevverted in the best of my specimens and appears as a sac-like body within the expanded portion of the penis-tip. The cavity of the sac-like part is partly filled by an irregular, opaque mass and opens freely to the exterior of the penis subapically. This orifice is either that part through which further eversion occurs or it is the ejaculatory pore. The opaque mass is probably semen.

*Atrium.*—The lobular structure noted in the mating process is formed by the eversion of the atrium and the "stimulator" contained in it. The latter merely forms part of the fleshy lobes and is thus not homologous to the stimulator of German malacologists, e.g., *Reizkörper* as exemplified by *Deroceras agreste* (L.). In mating-anatomies the entire structure appears as a fleshy, lobate



Fig. 5. A photograph of penis shown in Fig. 4. Note the papillae.

Figures 2-5 are from projections of whole-mounts preserved in canada balsam. The scale-lines show the equivalent of 2 mm.

Symbols: AAL, Anterior atrial lobe; AD, Atrial disk; EPT, Expanded penis tip; F, Foot; FO, Free-oviduct; H, Head; IM, Inner mass (semen?); LP, Large papilla; M, Mantle; P, Penis; PAL, Posterior atrial lobe; PO, Penis orifice; PR, Penis retractor muscle; PS, Penis sac (unevverted part of penis); PST, Penis stalk; SD, Spermathecal duct; SDO, Spermathecal-duct orifice. SP, Small papilla; V, Vagina; VD, Vas deferens; VO, Vagina-orifice.

disk; two of the lobes, the anterior and posterior, are (in my material) thicker and more prominent than the rest. The function of the organ remains to be determined; it may function as a neck shield which is gnawed at in preference to the adjacent structures. Such a defense structure (of tape like form) has been noted in the polygyrid *Allogona profunda* (Say). The extreme basal portion of the penis is continuous with the central portion of the disk, where the vaginal orifice is situated. The disk is apparently very sparsely papillate adjacent to the base of the penis.

*Female-organs.*—The form of the female organs in mating-anatomies is essentially the same as in resting ones, except that the eversion of the atrial structure brings the orifice of the vagina to the exterior. In mating-anatomies the penis occupies the vaginal cavity. The vagina is sigmoidal below its junction with the hermaphroditic duct or uterus. The tip of the deeply inserted penis rests near the lower flexure, while the orifice of the spermathecal duct is below the point of junction between the penis stalk and the expanded penis tip. It thus appears that part of the free oviduct below the sigmoid flexure is actually part of the vagina, and only the flexure and the remaining free parts can correctly be termed "free oviduct."

Few data were obtained in regard to reciprocity or non-reciprocity of coitus. In the mating-anatomies of two of the pairs coitus was clearly reciprocal, although in one pair the apical portion of the penis was yet unevverted. In the third pair the penis of one of the animals was incompletely extruded and but shallowly inserted into the mate's vagina; the penis of the other was wholly retracted. Inasmuch as coitus in landsnails sometimes does not begin simultaneously in the two mating animals, as in some species of *Helminthoglypta* (Webb 1942), the non-reciprocal relationship observed in the third pair is inconclusive.

Coitus seems to be quite prolonged. According to F. C. Baker (1902, p. 174) it has been observed to last for "... over ten hours. ..." Unfortunately I have obtained no supplementary data.

The matter of possible mating seasons likewise must await further investigation. The matings observed occurred under artificial laboratory conditions on October 2 and 23, 1941, and January 28, 1942. F. C. Baker (*op. cit.*) mentions May 18, 1897, but gives no information regarding the circumstances. My Loc. 2x specimens were collected September 11th, and the Wollen's Gardens material October 5, 1941. No matings were observed with the specimens held in confinement the previous winter. In a balsam mount of a mating-anatomy preserved *in toto*, uncalcified eggs are visible within the ovotestis duct; this was a reciprocal mating.

Should both eggs and sperm mature simultaneously, self-fertilization may take place. The known occurrence of habitual self-fertilization among gastropods, as in certain *Lymnaeae* (Crabb 1927, 1928), and the rather elaborate preventive mechanism in others, as in *Embletonia fuscata* Gould (Chambers 1934), make the investigation of this problem desirable.

### Summary

1. *Mollusca, Gastropoda, Pulmonata, Haplotrematidae*. The present contribution is a study of the mating of captive specimens of *Haplotrema (Geomene) concavum* (Say) with reference to the anatomy, behavior, and functioning of the sex organs.

2. In mating one animal mounts the other's shell. When over the aperture, the upper animal reaches downward and the lower upward. They begin gnawing at each other's foreparts, which become entwined. Copulation commences, following the eversion of penis and atrium, with the insertion of the penis into the vagina. About this time neck gnawing ceases.

F. C. Baker's ten-hour coitus duration record for the species remains un supplemented. Mating season data are given and the possibility of self-fertilization is considered.

3. The club-shaped, papillose penis is divided into a basal stalk and an ovoid apical part. The everted atrium appears as a fleshy, lobate disk continuous with the penis and vaginal orifice. The vagina extends from the orifice to the lower flexure and the free oviduct from there to the uterus.

4. The penis penetrates the vagina to the sigmoid flexure. The orifice of the spermathecal duct is below the tip of the inserted penis. It is suggested that the atrial disk has the function of a protective neck shield.

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# Biological Survey of the Bogs and Swamps in Northeastern Ohio\*

John W. Aldrich

## Introduction

The purpose of this study is to obtain as accurate a picture as possible of the composition and dynamics of the various biotic communities which make up the swamps and bogs (hydrosere) of northeastern Ohio, to show their successional relationship to each other, and to indicate their dependence on climatic and physiographic factors.

For valuable assistance during the course of this study the writer is indebted to several individuals: to Professor John H. Schaffner of the Department of Botany at Ohio State University, for identifying a large number of plants recorded in this paper; to Dr. Charles F. Walker and Milton B. Trautman of the Stone Laboratory at Put-in-Bay, Ohio, and Roger Conant of the Philadelphia Zoological Gardens, for their identifications of all specimens of amphibians, fishes, and reptiles, respectively; to B. P. Bole, Jr., Mammalogist of the Cleveland Museum of Natural History, for identifying the specimens of mammals, and for great assistance in coordinating the mammal population studies with the regular collecting program of that institution; to Mrs. Louise K. Aldrich for immeasurable assistance in computation of data; and especially to Dr. S. Charles Kendeigh, for his assistance and advice throughout the course of this study and the writing of the manuscript of this paper.

## DEFINITION OF TERMS

Because of the lack of agreement in the use of ecological nomenclature it seems desirable to define certain terms used in this paper which may not be entirely clear in the current literature. The definitions have been selected and modified when necessary from those appearing in the "Tentative Glossary of Ecological Terms" compiled by the Committee on Nomenclature of the Ecological Society of America (Revised list No. 1 and Preliminary list No. 2; 1934), from Clements (1916), Nichols (1923), Shelford (1913 and 1932), Smith (1928), Weaver and Clements (1929), Williams (1936), Carpenter (1938 and 1939), and Clements and Shelford (1939).

1. *Biome*.—The largest biotic community possible with a uniform type of life form presented by its primary climax dominant species in response to a certain set of climatic conditions. The writer sees very little difference between the biome and life zone concepts as applied today, even though they were

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originally arrived at by somewhat different approaches. The areas occupied by biomes correspond rather closely to the areas designated for the various faunal subdivisions of life zones. It would seem quite possible to revise the life zone concept to agree entirely with that of the biome and retain wherever applicable the terminology of the pioneer plant and animal geographers. The term "fauna" that has been used to designate a subdivision of a life zone obviously is not applicable to a biotic community which includes both plants and animals, and it is proposed that the term "biome" be substituted for it.

2. *Association*.—In the broad sense, a subdivision of a Biome in which the climax community contains the same species as primary dominants throughout. In the restricted sense, a climax community as distinct from an associates or developmental community.

3. *Associes*.—A developmental community in a sere, or the developmental equivalent of an association in which two or more primary dominants occur.

4. *Consociates*.—A geographic or local representative of an associates where only one primary dominant occurs.

5. *Facies*.—A subdivision of the associates in which there is a local difference in the relative abundance of the dominant species.

6. *Bog*.—A sere originating with a body of water such as a pond or lake (not a river) and ending in northern coniferous forest climaxes, characteristic of colder climates where peat accumulation is rapid.<sup>1</sup>

7. *Swamp*.—Since the term bog has been commonly restricted to hydrosere up to a boreal, coniferous climax, it would seem advisable to restrict<sup>2</sup> the term swamp to seres leading up to the more southern deciduous forest climaxes, characteristic of warmer climates where peat accumulation is slow or lacking. The terms moor and hydrosere are available for the more general meaning hitherto commonly given to swamp.

8. *Marsh*.—The portion of a swamp or bog dominated by grasses or grass-like vegetation.

9. *Biotic Succession*.—The process of orderly development of biotic communities on a bare area due largely to the activities of plants and animals themselves and successive replacement of one community by another until the climatic climax is reached.

10. *Climatic Succession*.—The change from one climatic climax and its particular set of seres to another due to major changes in climate.

11. *Primary Succession*.—Biotic succession (the prisere) originating on a primary bare area such as rock or water.

<sup>1</sup> It has been a common observation of the writer that peat accumulates in much greater quantities in cold than in warm climates, contrary to the assertions of most text books dealing with the formation of coal deposits.

<sup>2</sup> Recommendation of the author to remedy a bad confusion in the use of this term, a clear-cut definition of which is necessary in the organization of this paper.

12. *Secondary Succession*.—Biotic succession (the subser) which is subsequent to the destruction of part or all of the original plant and animal life of an area by man, fire, flooding, etc., without complete destruction of the substratum formed by biotic reactions of a former succession.

13. *Primary Dominant*.—A plant species which by abundance, shade cast, water absorbed, size, and other factors exerts the greatest influence in the biotic community.

14. *Secondary Dominant*.—A plant species which is less abundant and less influential than the primary dominant but which occurs in the same stratum.

15. *Subdominant*.—A species of plant which commonly exists under the dominating influence of the primary and secondary dominants.

16. *Predominant*.—Those animals that are most abundant in numbers and of greatest influence in the community.

17. *Member*.—Those animals in a community that are present in smaller numbers than predominants, and, therefore, of lesser influence.

18. *Life Form*.—The sum total of morphological, and physiological adaptations of plants and animals to their environment.

### Description of Area

#### LOCATION AND PHYSIOGRAPHY

The area of study herein spoken of as "northeastern Ohio" comprises Cuyahoga, Summit, Lake, Geauga, Portage, Ashtabula, and Trumbull Counties, in the extreme northeastern part of the State of Ohio. Roughly speaking, this is the land which lies between the cities of Cleveland and Akron on the west, and the Pennsylvania border on the east.

Within this area are portions of two of the physiographic provinces of the United States; the Central Lowlands and the Appalachian Plateau, the location of which together with their relationship to the more important hydrarch areas may be seen in Fig. 1. The "Till Plains" section of the Central Lowlands extends for a short distance into southwestern Cuyahoga County while the "Lake Plains" section of the same province occurs as a narrow belt along the shore of Lake Erie. The glaciated section of the Appalachian Plateau occurs to the south of the Lake Plain, and occupies fully seven-eighths of the entire area.

The water-shed divide between the St. Lawrence (Lake Erie) and the Ohio River drainage systems is about 30 miles south of Lake Erie in Summit, Portage, and Trumbull Counties. Small lakes and peat deposits frequently occupy depressions on or near the summit of this divide. This region was, in pre-glacial times, one of mature drainage with deep valleys and sharp ridges producing a much more rugged topography than now exists. The ice sheet which overrode the whole of northeastern Ohio in Pleistocene times rounded off the ridges and filled the old valleys with drift clays and sands so that



the present configuration is much less varied (Cushing, Leverett, and Van Horn, 1931, p. 14). It is in depressions in this glacial deposit, which fills the old valleys and which piled up on the north slope of the pre-glacial drainage divide, that water was frequently impounded and where most of the swamps of the region have developed.

The two great porous sandstones of the region, the Berea Grit and the Sharon Conglomerate are the source of many springs of copious and constant flow (Cushing, Leverett, and Van Horn, 1931, p. 61). This serves to keep the water levels of the swamps and bogs constant even during periods of deficient rainfall. Furthermore the heavy clay bottoms of most of the depressions prevent the rapid loss of water by seepage.

Mentor Marsh is the only swamp of importance that has developed in northeastern Ohio from so-called "ox-bow" ponds for the reason that the comparatively young rivers have not had time to develop the extensive flood plains necessary to the formation of this type of pond. No large lake shore or delta marshes occur at present in northeastern Ohio, such as have developed at the western end of Lake Erie.

No attempt was made to study the physico-chemical nature of the soils in the various hydrarch communities of northeastern Ohio, other than the determination of the hydrogen-ion concentration, which is frequently a very good indicator of other physico-chemical factors. The pH of soil samples was determined by means of a potentiometer-electrometer apparatus. In general the

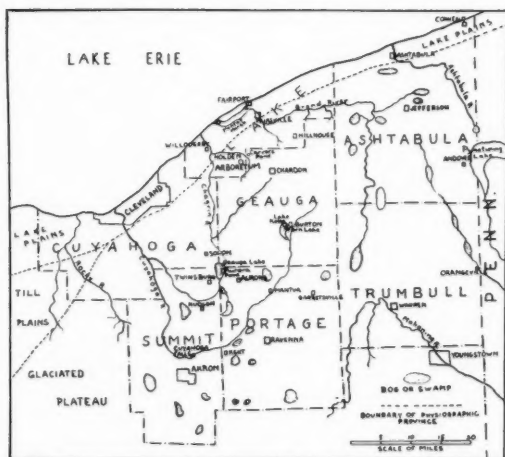


Fig. 1. The northeastern Ohio area showing the position of swamps and bogs (stippled) and physiographic provinces (outlined with a broken line). Political boundaries are marked with dots and dashes. Adapted from Dachnowski (1912) and Peattie (1923).

hydrogen-ion concentration was found to increase in progressing from open water to the swamp forest and to be higher in bog than in swamp communities. The results are given in Table 1. Some analyses of peat soils in northeastern Ohio have been made by Dachnowski (1912) and Clarke (1933), but much remains to be done, particularly with respect to the concentration, availability and balance of the elements essential to plant life in relation to the different communities.

TABLE 1.—Acidity of Substratum in Hydrarch Communities.

Community	Range of pH	Average pH
Nymphaea advena (Swamp or Bog)		
Consociates		
Soil (2 samples)	6.0-6.6	6.3
Water (4 samples)	4.6-6.0	5.4
Decodon-Typha (Swamp)		
Associates (6 samples)	4.1-5.8	4.8
Juncus-Scirpus (Swamp)		
Associates (8 samples)	4.4-5.0	4.7
Cephalanthus-Alnus (Swamp)		
Associates (4 samples)	4.7-5.8	5.3
Chamaedaphne calyculata (Bog)		
Consociates (9 samples)	3.2-3.8	3.5
Larix-Acer-Betula (Bog)		
Associates (15 samples)	3.0-4.7	3.4

A general survey of the various swamp and bog areas in northeastern Ohio (Fig. 1) was first made in 1930 and 1931. Then certain areas which seemed to be particularly well suited were chosen for intensive study. These were at Mentor Marsh, Aurora Pond and Lake Kelso, and the Holden Arboretum (Fig. 2), the locations of which are shown in Fig. 1.

#### CLIMATE

The present day hydrarch communities in northeastern Ohio owe their distinctive characters both to the post-glacial and present climate of the region, as well as to the physiographic factors mentioned in the last section. Studies by Sears (1930, 1931, 1932) seem to indicate that in northeastern Ohio since Pleistocene times there have been four successive climatic periods recognizable by the type of vegetation covering the land: a cold damp, a cool dry, a warm dry, and finally a warm damp period. The work of Voss (1934), Fuller (1935), and others in the Lake Michigan region tends to discount the fluctuation in moisture, but show quite definitely a cold period indicated by spruce and fir followed by a much longer, warmer period indicated by deciduous tree pollen, chiefly oak. A very recent cooler trend is indicated by the increase

in spruce pollen in the upper peat strata in the region of intergradation between coniferous and deciduous forests.



Fig. 2. Special Study Areas. a, Norton's Pond, Mentor Marsh. b, Aurora Pond. c, Fern Lake in the Lake Kelso Area. (Photographed by A. B. Williams.)

The present climate of any point in northeastern Ohio is influenced strongly by three factors: proximity to Lake Erie, topography, and vegetation. Such local extremes of climate as are found in northeastern Ohio do not exist in any other part of this State. The average length of growing season varies from 202 days at Cleveland on the lake shore to 135 days at Garrettsville on the Appalachian Plateau; the average mean annual temperature from 49.2° F. to 47.5° F. at these stations. The average annual precipitation varies from 33.39 to 40.18 inches; and the average annual snowfall from 29.7 to 63.3 inches between lake shore and plateau stations. Kirtland (1874) long ago called attention to the moderating influence of Lake Erie upon the temperature of the land directly south of it, pointing out the resulting southern type of indigenous vegetation and animal life along its south shore. The lake is also responsible for the extreme cloudiness which affects the country for a short distance south of it (Mosely 1897). Unfortunately there are no comparable data on amount of sunshine for any station in northeastern Ohio other than Cleveland for comparison. There is, however, a very considerable amount of seasonal variation in this factor registered at that station (74% of possible sunshine in July and 24% in December).

A hygrothermograph for continuous recording of temperatures and relative humidities was established in a shelter supported on piles about one foot above high water in a cat-tail community at Aurora Pond, elevation 1,000 feet above sea level on the Appalachian Plateau and 20 miles distant from Lake Erie. In the same region three maximum-minimum thermometers, of the type manufactured by the Taylor Instrument Company, were placed about five feet above the ground, one in a bog-shrub community, attached to the north side of a two-inch alder stem and two in a red maple-yellow birch bog forest community attached to the north side of tree trunks. Another maximum-minimum thermometer was similarly placed in a tamarack community at Lake Kelso, 1,100 feet above sea level on the Appalachian Plateau and 22 miles from the shore of Lake Erie. Weekly records were obtained from these instruments except when they were interfered with by accident or theft (accounting for the gaps) from February 1934 to January 1935 (Figs. 3 and 4). The data in Fig. 4 show that modification of air temperature is brought about by the vegetation of a community, particularly during the season of maximum leafage. The greatest effect is produced by the forest in which the plants are the largest, the least by the marsh where the plants are the smallest. A greater influence seems to be exerted by vegetation upon maximum temperature than upon the minimum.

The average weekly relative humidity based on hourly readings from the hygrothermograph in the cat-tail community at Aurora Pond is shown in Fig. 5. A comparison of this graph with that of Williams (1936, p. 10) compiled on the basis of the same type of data from the same instruments operated in a beech-maple climax community, shows that an open marsh may have a relative humidity which averages only about 6 percent lower than that in the interior of a heavy climax forest which is located at about the same

elevation and not more than 16 miles distant. The average annual relative humidity for the Aurora Pond cat-tail community, based on the hygrothermograph records, was 75 percent.

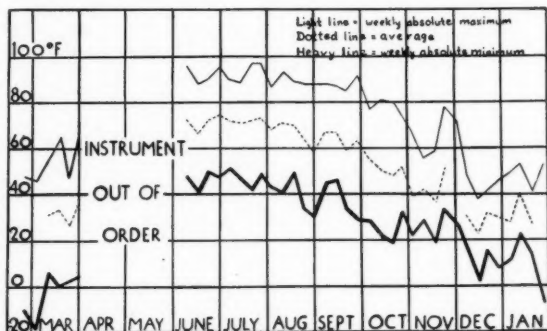


Fig. 3. Maximum, minimum and average weekly air temperatures in a cattail (*Typha latifolia*) community at Aurora Pond, February 1934 to January 1935.

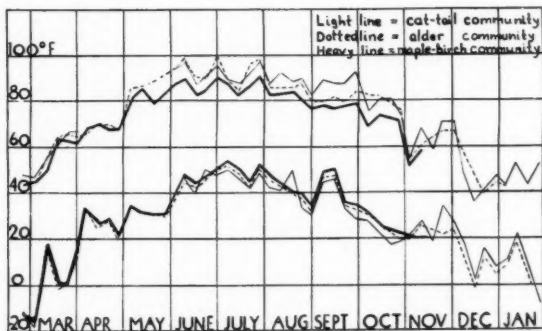


Fig. 4. Weekly absolute maximum and minimum air temperatures in three different communities at Aurora Pond, February 1934 to January 1935.

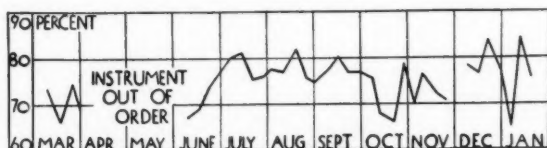


Fig. 5. Average weekly relative humidities on basis of hourly readings in a cat-tail (*Typha latifolia*) community at Aurora Pond, March 1934 to January 1935.

Seventy-two scattered determinations of relative humidity by means of a cog psychrometer in various communities at Aurora Pond and Lake Kelso taken at as nearly comparable times as possible, indicate that the swamp loosestrife and yellow birch-red maple communities have approximately the same diurnal relative humidities. Both of these communities showed humidities during daylight approximately 15 percent higher than simultaneous readings in the cat-tail community in which the hygrothermograph records were made. This difference would be considerably less if determined on a 24 hour a day basis, since nocturnal humidities of the three communities would undoubtedly approximate one another much more closely. Compared with the results obtained by Williams (1936, p. 10), it seems likely that the average summer relative humidities of the swamp loosestrife and red maple-yellow birch communities are similar to those in the beech-sugar maple climax.

Although the amount of precipitation which actually reaches the earth in a hydrarch community is not as important as in the case of a well-drained upland community, since the water collected in a swamp is distributed by seepage to all parts, an attempt was nevertheless made to measure the amount of rainfall in both marsh and bog forest at Solon Bog by means of standard rain gauges operated from April 28 to November 3, 1934. The result was 15.1 inches for the marsh (common rush-wool grass community) as against 13.9 for the bog forest (red maple-yellow birch community), or 92 percent as much effective rainfall in the forest as in the marsh. Another rain gauge operated in a bog heath (leatherleaf community) at Lake Kelso, recorded 20.6 inches during the period from May 2 to October 10, 1934, thus showing a considerably greater precipitation for that area than for Aurora Pond.

Evaporation combines the effect of relative humidity, wind velocity and the temperature into one measurement of effective controlling factors. Table 2 gives the average evaporation in the hydrarch communities obtained from Livingston standardized spherical atmometers operated in duplicate during the summer of 1934. It also contains comparative results derived from records obtained with the same type of instruments by Williams (1936, p. 16) in a beech-maple climax forest and an open field community, 16 miles distant from Aurora Pond and during exactly the same periods of time as the writer's evaporation studies at that station. It is interesting to note that the open field community has an evaporation rate 2.6 times that of the *Juncus-Scirpus* community, which probably has the highest rate of any in the swamp. The *Fagus-Acer* community has an evaporation rate almost identical to the *Typha* and 1.8 times greater than the *Acer-Betula* bog forest. As may be noted from the table it is possible to have a very marked local variation in the evaporating power of the air in a community, depending upon variation of the vegetation immediately surrounding the atmometer. This is particularly noticeable in the rush community where the dominant vegetation is low and sparse and, therefore, the ground cover plays a comparatively much greater role in controlling the evaporation.

Evaporation data obtained by Dickey (1909, p. 22) for two bog communi-

TABLE 2.—Evaporation Rates in Various Communities at Lake Kelso and Aurora Pond, and in a Beech-Maple Forest and Open Field at North Chagrin Reservation during the Summer of 1934.

Community and Locality	Location of Atmometer	Time of Operation	Aver. weekly evaporation in cc. per hour for each Atmometer	Aver. weekly evaporation in cc. per hour for both Atmometers
<i>Typha latifolia</i> community at Aurora Pond	Instrument a. In a small opening in cat-tails. Ground cover dense growth of <i>Persicaria</i> , <i>Bidens</i> and <i>Cicula bulbifera</i> (not over top of evaporating surface).	July 7 to Sept. 1	.255	
	Instrument b. At edge of opening in cat-tails. Slight ground cover of <i>Bidens</i> (not over top of porous bulb).	July 7 to Sept. 1	.277	.266
<i>Juncus effusus</i> - <i>Scirpus cyperinus</i> community at Aurora Pond	Instrument a. Under heavy cover of grass <i>Bidens</i> , <i>Cicuta bulbifera</i> and <i>Sagittaria latifolia</i> .	July 14 to Sept. 1	.244	
	Instrument b. Under light cover of grass <i>Bidens</i> and <i>Tracaulon sagittatum</i> .	July 14 to Sept. 1	.342	.293
<i>Chamaedaphne calyculata</i> community at Lake Kelso	Instrument a. Bottle buried in Sphagnum and <i>Carex</i> among <i>Chamaedaphne</i> , <i>Anchislea virginica</i> , <i>Decodon</i> .	Aug. 1 to Sept. 5	.158	
	Instrument b. Bottle buried in Sphagnum among <i>Chamaedaphne</i> and <i>Decodon</i> .	Aug. 1 to Sept. 5	.171	.165
<i>Acer rubrum</i> - <i>Betula lutea</i> community at Aurora Pond	Instrument a. Under <i>Ilex verticillata</i> , <i>Viburnum dentatum</i> , <i>Acer rubrum</i> , <i>Betula lutea</i> , and <i>Nyssa sylvatica</i> . No ground cover	July 7 to Sept. 1	.162	
	Instrument b. Among <i>Osmunda cinnamomea</i> under <i>Nyssa sylvatica</i> , <i>Betula lutea</i> , and <i>Acer rubrum</i> .	July 7 to Sept. 1	.156	.159
<i>Fagus grandifolia</i> - <i>Acer saccharum</i> community at North Chagrin <sup>1</sup>		July 9 to Sept. 1		.286
	Open Field community at North Chagrin <sup>1</sup>	Aug. 1 to Sept. 1		.771

<sup>1</sup> From Williams (1936).



ties at Buckeye Lake, Ohio, and those of Sears (1916, p. 97) for several marsh communities at Cedar Point, Ohio, are materially greater than the data obtained by the writer in presumably comparable habitats. The fact that both Dickey and Sears used cylindrical atmometers while those in the present study were spherical undoubtedly accounts for much of the discrepancy.

#### THE ORIGINAL BIOTA AND ITS SUBSEQUENT MODIFICATION

The area considered as northeastern Ohio in this paper is within the Deciduous Forest Biome (Clements and Shelford, 1939), but lies athwart the line separating two life zones, the Transition and the Upper Austral, represented in this region by the Alleghanian and Carolinian Faunas respectively, according to the map of Merriam, Bailey, Nelson, and Preble (1910). This condition is shown in the biome map by Pitelka (1941) as an extension into northeastern Ohio of the broad ecotone between the Coniferous Forest and Deciduous Forest Biomes. The entire area falls within the Mixed Mesophytic Forest region of Braun (1938), and at least the Appalachian Plateau portion is characterized by the Beech-Maple Association Segregate of Braun (1938), or *Fagus-Acer* Association of Weaver and Clements (1929). The beech and sugar maple climax forest of this region (Fig. 6a) was reported on in detail by Williams (1936). Remnants of forest which seem to be representative of the Oak-Hickory Association are to be found chiefly in the Till Plains and Lake Plains areas, Oak-Chestnut Association on the ridge tops and Pine-Hemlock Association on ravine banks, moist sandstone outcrops and in mature bog forest areas. The fragments of white pine and hemlock forest in northeastern Ohio are considered as relics of a former southward extension of the northern climax (Fig. 6b) called the Lake Forest or *Pinus-Tsuga* Formation by Weaver and Clements (1929) and the Eastern Hemlock-White Pine-

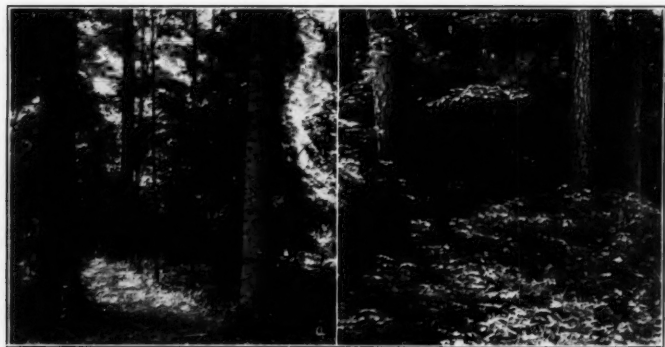


Fig. 6. Comparison of Typical Beech-Maple (*Fagus-Acer*) and Pine-Hemlock (*Pinus-Tsuga*) Associations. (a) Climax forest of Beech and Sugar Maple at North Chagrin Reservation near Cleveland, Ohio. (Photo by A. B. Williams). (b) Climax forest of Red Pine and White Pine at Timagami, Ontario.

Northern Hardwood Forest by Nichols (1935). This type of post-climax is being studied in northeastern Ohio by B. P. Bole, Jr., of the Cleveland Museum of Natural History. The admixture of climax coniferous forest, together with its associated seral communities, with the deciduous forest units is probably the reason that this area has previously been considered as partly within the Transition Life Zone, which is essentially an ecotone. Unlike some of his colleagues the writer thinks that it is possible to bring together the life zone and biome concepts and unify the nomenclature, using the life zone names where applicable. Thus biomes would replace faunas as subdivisions of life zones. On this basis northeastern Ohio is entirely within the Eastern Deciduous Forest Biome of the Upper Austral Life Zone, but still contains scattered post-glacial relics of the Northern Conifer-Deciduous Forest Ecotone and of the Appalachian Montane Forest of the Transition Life Zone. It should be noted that the present author's concept of the Transition Life Zone is not entirely that of Merriam and his followers, but includes the ecotones between the northern conifer and subalpine forests on the one hand and deciduous forests and grassland on the other. My concept of the Transition Life Zone, therefore, encompasses the various forest climax communities that have been called Lake Forest, Pine-Hemlock-Northern Hardwood Forest, the various Montane Forests, and the Aspen Parklands.

That northeastern Ohio was not entirely forested when the white man first came to this region is attested in the finding by Sears (1926a, p. 135), in the accounts of the first surveyors, of records of "natural wet prairies," along the drainage divide in Summit, Portage, and Trumbull counties. These "wet prairies" marked the courses of deeply buried and silted preglacial drainage valleys, or the sites of postglacial lakes, and were (Sears, 1926b, p. 129) "equivalent to wet meadow generally consisting of sedges, rushes, and grasses, and the term was sometimes extended to include cat-tail and pickerel-weed 'associations' and not infrequently used to indicate bog meadows, i. e., 'cranberry prairie.'" These so-called "wet prairies" of the early surveyors were obviously preforest stages of the hydrarch succession.

The animal life of northeastern Ohio, as it existed when the country was first settled by the white man, was very sketchily recorded by the early settlers, only the more obvious species, or those which played a part in the economics of the human community, being noticed. We are, however, fortunate to have the benefit of the information, scanty as it is, gathered by the well-known naturalist Dr. Jared P. Kirtland, whose observations in northeastern Ohio dated back to 1810 or almost to the time of the first settlement (Kirtland 1838 and Christy 1936).

Of the original animal life, probably the most important from the standpoint of influence in hydrarch succession was the beaver which Kirtland says was extirpated before 1838, although it was said to have existed formerly in great numbers (Bull, 1858). This species is capable of initiating secondary succession on a large scale through changing of water levels and denudation of flora. It is difficult to estimate to what extent the original hydrarch com-

munities of northeastern Ohio owed their condition to beaver activity, but the possibilities are very good that much of the apparently secondary hydrarch succession such as "wet prairies," not of the boreal or "cranberry prairie" type, mentioned by Sears (1926a, p. 129) as occurring in northeastern Ohio, owe their origin to beaver activity. For further discussion of primary versus secondary succession see following section on "biotic succession."

Of the original fauna described by the early settlers, the elk, black bear, timber wolf, Canada lynx, fisher, otter, beaver,<sup>1</sup> swallow-tailed kite, turkey, passenger pigeon, raven, and timber rattlesnake, have long since ceased to exist in northeastern Ohio, while the white-tailed deer, varying hare, and porcupine, with the possible exception of the deer, if present at all, are represented only by occasional stragglers from the forests of the Pennsylvania mountains to the east. The Virginia white-tailed deer seems to have been on the increase during the last few years, and has been reported on several occasions recently; in fact no less than thirteen individuals were seen together in a comparatively forested region in southeastern Kirtland Township, Lake County, in the winter of 1938-39. The slate-colored junco as a breeding species has apparently been greatly reduced in numbers since Kirtland's time with the removal of the greater part of the "dark beech woods" from the region. The gray squirrel as well as many other typical species of the beech-maple forest are without much doubt much less common now than in pioneer days. On the other hand, the available records seem to indicate a radical increase of species characteristic of the more open oak-hickory woods, marsh and other secondary succession communities, such as the red fox, New York weasel, fox squirrel, muskrat, marsh hawk, cardinal, and American crow. The complete elimination of such a large part of the original fauna must have left vacant a considerable number of niches in the few remaining areas of the original communities. To what extent these niches have been occupied by the new species would be hard to estimate. It is very likely, however, that the white man has more than filled the niche formerly occupied by the larger carnivores!

The history of northeastern Ohio since the early part of the 19th century has been one of gradual opening up of the land for farming. Most of the upland hardwood timber was cut off rather quickly and the land utilized for crop raising and pasture. The swamp and bog forests were not exploited as quickly since their characteristically soft wood timber was not commercially valuable. More recently the value of peat land for crop raising has been appreciated and much swamp land and bog land has been cut off, drained, and cultivated. The growth of great industrial centers in the northeastern Ohio region, making necessary increased water storage for power and for consumption by large human populations, has resulted in the utilization of some of the large swamp basins for reservoirs. The recreational possibilities of many of the hydrarch areas still containing sizable bodies of open water have been realized and the natural conditions have been greatly altered by development of

1 After being considered extinct since 1838 a specimen was found dead in 1939 near Cleveland by State Game Protector Herbert Cannell, who had previously found the tracks of the animal on several occasions.

summer resorts and amusement parks. In the years that have elapsed since the appearance of Dachnowski's (1912) report on the peat deposits of Ohio, profound changes have been wrought in the biotic communities of most of the hydrarch areas of northeastern Ohio. Most of the larger areas such as the Pymatuning and Orwell-Bloomfield Bogs have been completely destroyed. Solon Bog has been greatly modified by artificial changing of the water level of Aurora Pond and by fires; the interesting boreal relic communities of the portion around Geauga Lake having been destroyed when that area was converted into an amusement park. Of all the northeastern Ohio hydrarch areas described by Dachnowski that the writer has had occasion to examine carefully, the Bogs surrounding Lake Kelso (Bradley Pond) and Fern Lake (Everett Pond) near Burton have been the best preserved. These areas which occupy a series of depressions close together in the same valley in southwestern Burton Township, undoubtedly now contain the best examples of relic boreal hydrarch communities to be found in northeastern Ohio.

### Biotic Succession

#### METHODS OF STUDY

Transect studies were made at Mentor Marsh (Fig. 2a), where the succession is chiefly of the swamp type (more southern); at Lake Kelso (Fig. 2c), a good example of bog (boreal) succession; and at Aurora Pond (Fig. 2b), where both bog and swamp type are represented and a large percentage of secondary succession conditions exist resulting from fires and artificial raising of the water level. The method was to mark off a string into meter sections and extend this in a straight line from open water onto dry land. The species within arm's reach (about 1 meter) on either side of each meter section of the string were then recorded with notes as to their relative abundance. The result was a record of species that occurred in a belt transect made up of a chain of quadrangles 1 meter long by 2 meters wide. In Figs. 7, 8, 9, illustrating the results of the transect studies, sectors showing virtually the same composition are combined to avoid needless repetition. A modification of this method (Fig. 10) was also used to determine the succession of the small nocturnal mammal population. Groups of three mouse traps were set out, arranged roughly in an equilateral triangle, not more than 3 meters to the side, centering around each 10-meter mark along the transect string. The transect method was found not feasible for forms other than plants and small mammals because of the small amount of data obtained for any one transect.

Study of changes in the species composition of the same experimental area from year to year was made possible by comparison of vegetation maps and censuses of organisms in certain experimental areas of known size at Aurora Pond, made in different years from 1932 to 1936 inclusive (in the case of birds and mammals through 1939). A severe fire at Aurora Pond, cutting of trees and shrubs at Lake Kelso, and flooding at both Aurora Pond and the Holden Arboretum, have made it possible also to study the initiation of succession after denudation arising from these causes, and to trace its course

for two to three years. Thus the three methods of "inference," "sequence," and "experiment" (Clements 1916) were all used.

#### BELT TRANSECTS

*Mentor Marsh, 1931.*—A transect (Fig. 7) was made at Norton's Pond, Mentor Marsh, in the autumn of 1931, extending from a hawthorn pasture on one side of the pond across open water to a pin oak swamp forest on the other side.

FALLOW FIELD	<u>CRATAEGUS</u> SP. <u>MALUS</u> SP.	4 METERS
FOREST	<u>SALIX</u> <u>INIGRA</u>	34 M.
SHRUB	<u>CERHALANTHUS</u> <u>OCCIDENTALIS</u>	14 M.
EMERGING PLANT	<u>DECODON</u> <u>VERTICILLATUS</u>	21 M.
FLOATING PLANT	<u>NYMPHAEA</u> <u>ALBIDNA</u> <u>CERATOPHYLLUM</u> <u>DEMERSUM</u>	30 M.
SUBMERGED PLANT	<u>CERATOPHYLLUM</u> <u>DEMERSUM</u>	40 M.
FLOATING PLANT	<u>NYMPHAEA</u> <u>ALBIDNA</u> <u>PERSICARIA</u> <u>HYDROPERODES</u> <u>CERATOPHYLLUM</u> <u>DEMERSUM</u>	100 M.
EMERGING PLANT	<u>DECODON</u> <u>VERTICILLATUS</u>	15 M.
SHRUB	<u>CERHALANTHUS</u> <u>OCCIDENTALIS</u>  <u>SALIX</u> <u>INIGRA</u>	35 M.
FOREST	<u>QUERCUS</u> <u>PALLUSTRAIS</u>	12 M.

Fig. 7. Simplified plant belt transect at Norton's Pond, Mentor Marsh in October, 1931. Underlined species are primary dominants in the particular sector in which they are listed.

Lake Kelso and Fern Lake, 1934-1936.—In August and September, 1934, four transects were made at Fern Lake and Lake Kelso. In August, 1936, one transect was made at Fern Lake in approximately the same place as one of those made two years previously for the sake of determining what changes, if any, had taken place during the two intervening years. The transect at Lake Kelso and a typical example of one at Fern Lake are shown in Fig. 8.

FERN LAKE		LAKE KELSO	
↑	Open Water	↑	* <i>Brazenia schreberi</i>
EMERGING 1 meters	* <i>Decodon verticillatus</i>	EMERGING 1 meters	* <i>Decodon verticillatus</i> <i>Triadenum virginicum</i> <i>Dryopteris thelypteris</i> <i>Boehmeria cylindrica</i> <i>Sagittaria latifolia</i> <i>Osmunda regalis</i> <i>Chamaedaphne calyculata</i> <i>Sphagnum</i> Sp.
EMERGING 2 meters	* <i>Decodon verticillatus</i> <i>Triadenum virginicum</i> <i>Bidens</i> Sp. <i>Carex howei</i>	EMERGING 2 meters	* <i>Chamaedaphne calyculata</i> <i>Aronia atropurpurea</i> <i>Decodon verticillatus</i> <i>Osmunda regalis</i> <i>Dryopteris thelypteris</i> <i>Boehmeria cylindrica</i> <i>Sagittaria latifolia</i> <i>Sphagnum</i> Sp. <i>Oxycoccus macrocarpus</i>
HEATH 3 meters	* <i>Chamaedaphne calyculata</i> <i>Anchistea virginica</i> <i>Decodon verticillatus</i> <i>Sphagnum</i> Sp.	HEATH 3 meters	* <i>Vaccinium corymbosum</i> <i>Aronia atropurpurea</i> <i>Larix laricina</i> (small) <i>Betula lutea</i> (small) <i>Chamaedaphne calyculata</i> <i>Decodon verticillatus</i> <i>Peltandra virginica</i> <i>Oxycoccus macrocarpus</i> <i>Sagittaria purpurea</i> <i>Fissipes adules</i>
HEATH 4 meters	* <i>Chamaedaphne calyculata</i> * <i>Gaylussacia baccata</i> <i>Anchistea virginica</i> <i>Sphagnum</i> Sp.	HEATH 4 meters	* <i>Larix laricina</i> <i>Sphagnum</i> Sp.
HEATH 5 meters	* <i>Gaylussacia baccata</i>	SHRUB 5 meters	* <i>Nemopanthus mucronata</i> * <i>Vaccinium corymbosum</i> <i>Sphagnum</i> Sp. <i>Gaultheria procumbens</i> <i>Osmunda cinnamomea</i> <i>Coptis trifolia</i> <i>Unifolium canadense</i> <i>Acer rubrum</i> (seedlings) <i>Aronia atropurpurea</i> (seedlings)
SHRUB 6 meters	* <i>Larix laricina</i> <i>Gaylussacia baccata</i>	SHRUB 6 meters	* <i>Larix laricina</i> <i>Sphagnum</i> Sp.
SHRUB 7 meters	* <i>Larix laricina</i> <i>Nemopanthus mucronata</i> <i>Vaccinium corymbosum</i> <i>Acer rubrum</i> (seedlings) <i>Betula lutea</i> (seedlings) <i>Unifolium canadense</i> <i>Coptis trifolia</i> <i>Dryopteris spinulosum</i>	TALL 7 meters	* <i>Nemopanthus mucronata</i> * <i>Vaccinium corymbosum</i> <i>Sphagnum</i> Sp. <i>Gaultheria procumbens</i> <i>Osmunda cinnamomea</i> <i>Coptis trifolia</i> <i>Unifolium canadense</i> <i>Acer rubrum</i> (seedlings) <i>Aronia atropurpurea</i> (seedlings)
FOREST 8 meters	* <i>Larix laricina</i> * <i>Betula lutea</i> * <i>Acer rubrum</i> (Subdominants as above)	FOREST 8 meters	* <i>Larix laricina</i> * <i>Acer rubrum</i> <i>Vaccinium corymbosum</i> <i>Nemopanthus mucronata</i> <i>Osmunda cinnamomea</i> <i>Sphagnum</i> Sp. <i>Unifolium canadense</i>
FOREST 9 meters	* <i>Betula lutea</i> * <i>Acer rubrum</i> <i>Vaccinium corymbosum</i> <i>Nemopanthus mucronata</i> <i>Ilex verticillata</i> <i>Dryopteris spinulosum</i> <i>Unifolium canadense</i> <i>Coptis trifolia</i> <i>Medeola virginiana</i> <i>Gaultheria procumbens</i> <i>Mitchella repens</i>	SHRUB 9 meters	* <i>Toxicodendron vernix</i> * <i>Nemopanthus mucronata</i> * <i>Vaccinium corymbosum</i> <i>Sphagnum</i> Sp. <i>Gaultheria procumbens</i> <i>Osmunda cinnamomea</i> <i>Coptis trifolia</i> <i>Medeola virginiana</i> <i>Acer rubrum</i> (seedlings) <i>Unifolium canadense</i>

Fig. 8. Simplified plant belt transects at Lake Kelso and Fern Lake made in 1934. Starred species are primary dominants in the particular sector in which they occur. Others are listed in approximate order of abundance and dominance.

*Aurora Pond, 1932, 1934, 1936.* — In 1932, a transect was plotted at Aurora Pond from a water-lily zone to an open field, and in 1936 a transect was made at exactly the same location (Fig. 9). The water level of Aurora Pond had been raised about 1.5 feet (46 cm.) in 1925 so that these two

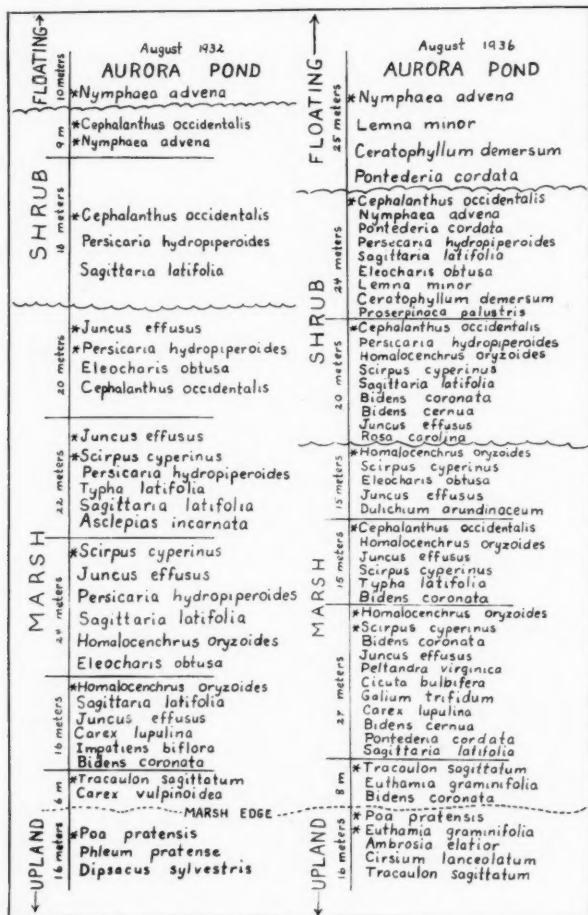


Fig. 9. Simplified plant belt transects at Aurora Pond made in the same location in 1932 and 1936. Starred species are primary dominants in the particular sector in which they occur. Others are arranged in approximate order of abundance and dominance.



transects are of primary importance in showing the rapid changes taking place in secondary succession of this sort. Most noticeable is the rapid encroachment of buttonbush on the marsh and the increase in the width of the shrub belt

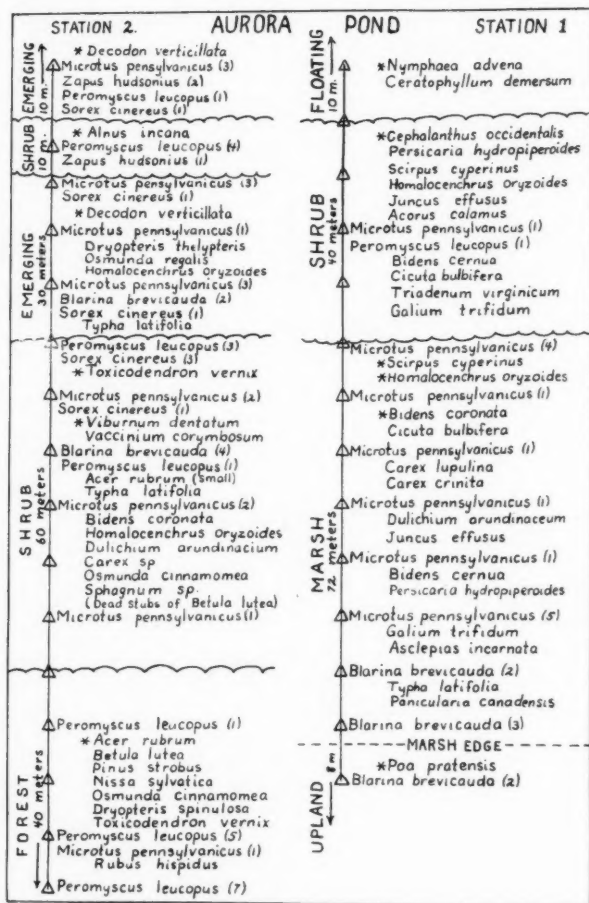


Fig. 10. Mammal trapping transects superimposed on plant belt transects at Aurora Pond in 1934. Triangles indicate location of sets of three mammal traps operated for 12 nights in October. Starred species are primary dominants in the particular sector in which they occur. Other plants are listed in approximate order of abundance and dominance in September and October.

despite the fact that it is being killed back on the pond side by the raised water level. These changes are also shown in Fig. 11.

In 1934 two belt transects (Fig. 10) were made at Aurora Pond primarily for the purpose of getting small mammal data. Transect 1 was laid out from the water-lily to the dry field zone in the experimental area at Stations 1 (Fig. 11), and transect 2 from the swamp loosestrife to the bog forest zone at Station 2 (Fig. 11).

#### SUCCESSION AT AURORA POND, 1932 TO 1936

In 1932 two experimental areas were selected at Aurora Pond. These were carefully mapped with the help of aerial photographs, taken from a height of one mile, which showed rather clearly the distribution of the major plant communities. By measuring the same distances on the ground and on the photographs it was possible to compute the scale. A map (Fig. 11) was

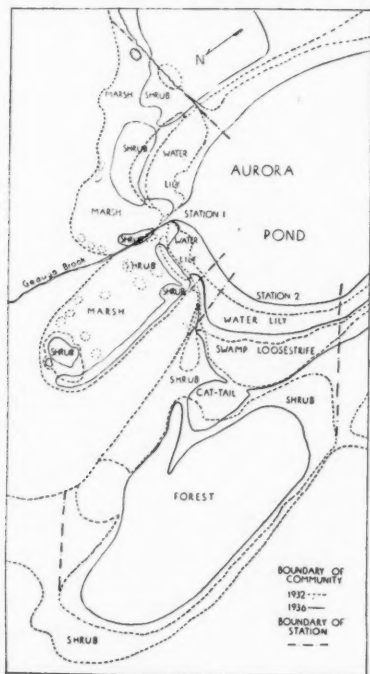


Fig. 11. Experimental Areas at Aurora Pond showing changes in areas of major communities from 1932-1936. Decrease in certain shrub and forest areas due to fires, and increase in other community areas resulting from succession is noticeable.

drawn to an accurate scale by means of a pantograph from the original aerial photographs. The changes in the vegetation occurring between 1932 and 1936 were plotted from studies on the ground.

#### INITIATION OF SUCCESSION AFTER DENUDATION

*Holden Arboretum, 1934-1936.*—In August 1934 the vegetation, bird and mammal life of a swampy area of about one acre in the Holden Arboretum was censused. Then in the autumn of the same year an earthen dam was built across the drainage outlet. This raised the water level to about 1 meter above the surface of the peat and increased the area covered by water to 2 acres (0.8 hectares) during the following winter. Throughout the whole of 1935 the water level did not recede more than 6 inches (15 cm.). Most of the herbaceous plant life which had been present in 1934 was completely exterminated.

Table 3 shows the original populations in 1934 and the changes in populations during the years following flooding. Common names of species are available in Table 8.

TABLE 3.—Succession at Holden Arboretum.

Species	Before flooding	After flooding			
	1934	1935	1936	1937	
Plants					
<i>Acer rubrum</i> .....	x	x			
<i>Acer saccharinum</i> .....	x	x			
<i>Ulmus americana</i> .....	x	x			
<i>Betula lutea</i> .....	x				
<i>Quercus palustris</i> .....	x				
<i>Sambucus canadensis</i> .....	x				
<i>Salix discolor</i> .....	x	x			
<i>Rosa carolina</i> .....	x	x	x	x	
<i>Vaccinium corymbosum</i> .....	x	x			
<i>Toxicodendron vernix</i> .....	x				
<i>Viburnum dentatum</i> .....	x				
<i>Cephalanthus occidentalis</i> .....	x	x	x	x	
<i>Ilex verticillata</i> .....	x	x	x	x	
<i>Sphagnum</i> sp. ....	x				
<i>Rubus hispidus</i> .....	x				
<i>Juncus effusus</i> .....	x	x	x	x	
<i>Scirpus cyperinus</i> .....	x	x	x	x	
<i>Scirpus lineatus</i> .....	x	x	x	x	
<i>Carex lupulina</i> .....	x		x	x	
<i>Dryopteris thelypteris</i> .....	x		x	x	
<i>Onoclea sensibilis</i> .....	x		x	x	
<i>Impatiens biflora</i> .....	x	x	x	x	
<i>Carex scoparia</i> .....		x	x	x	
<i>Eleocharis obtusa</i> .....		x	x	x	
<i>Cyperus strigosus</i> .....		x	x	x	
<i>Typha latifolia</i> .....		x	x	x	

TABLE 3.—Succession at Holden Arboretum (Continued)

Species	Before flooding	After flooding		
	1934	1935	1936	1937
<i>Bidens frondosa</i> .....		x	x	
<i>Lemna minor</i> .....		x	x	x
<i>Isnardia palustris</i> .....		x	x	x
<i>Sparganium angustifolium</i> .....			x	x
<i>Carex crinita</i> .....			x	
<i>Persicaria punctata</i> .....			x	x
<i>Persicaria pennsylvanica</i> .....			x	
<i>Potamogeton pusillus</i> .....			x	x
<i>Philotria canadensis</i> .....			x	x
<i>Naia flexilis</i> .....			x	x
<i>Homalocenchrus oryzoides</i> .....				x
Animals				
<i>Melospiza melodia</i> .....	x			x
<i>Dumetella carolinensis</i> .....	x			
<i>Geothlypis trichas</i> .....	x	x	x	x
<i>Peromyscus leucopus</i> .....	x		x	
<i>Microtus pennsylvanicus</i> .....	x	x	x	x
<i>Turdus migratorius</i> .....		x		x
<i>Agelaius phoeniceus</i> .....		x	x	x
<i>Butorides virescens</i> .....		x	x	x
<i>Anas platyrhynchos</i> .....		x	x	
<i>Natrix sipedon</i> .....		x	x	x
<i>Triturus viridescens</i> .....		x	x	x
<i>Rana clamitans</i> .....		x	x	x
<i>Rana sylvatica</i> .....		x	x	x
<i>Hyla crucifer</i> .....		x	x	x
<i>Hyla versicolor</i> .....		x	x	x
<i>Pseudacris triseriata</i> .....		x	x	x
<i>Ondatra zibethica</i> .....		x	x	x
<i>Mustela vison</i> .....		x	x	
<i>Condylura cristata</i> .....			x	x
<i>Podilymbus podiceps</i> .....			x	x
<i>Aix sponsa</i> .....			x	x
<i>Tyrannus tyrannus</i> .....			x	x
<i>Chrysemys picta</i> .....			x	x
<i>Bufo americanus</i> .....			x	x
<i>Rana palustris</i> .....			x	x
<i>Rana pipiens</i> .....			x	x
<i>Rana catesbeiana</i> .....			x	x
<i>Sorex cinereus</i> .....				x
<i>Dendroica aestiva</i> .....				x

*Aurora Pond.* — During the autumn of 1933 a fire at Aurora Pond destroyed considerable areas of forest and shrub communities. In some cases the fire merely burned to the surface of the peat, but in others the peat was consumed to a depth of about a meter. Recolonization in the burned shrub community of Station 1 and succession during the ensuing years is indicated in Table 4.

TABLE 4.—Succession After Destruction of a Swamp Shrub Community at Aurora Pond by Fire in Autumn of 1933.

Species*	1934	1936	1938
<b>Plants</b>			
Filamentous green algae .....	×		
<i>Bidens coronata</i> .....	×		
<i>Bidens cernua</i> .....	×		
<i>Populus tremuloides</i> .....	×	×	
	(seedlings)	(marsh edge)	
<i>Salix amygdaloides</i> .....	×	×	×
	(seedlings)	(1 meter high)	less abundant
<i>Typha latifolia</i> .....	×	×	×
		much more abundant	primary dominant
<i>Cyperus strigosus</i> .....	×		
<i>Echinochloa crus-galli</i> .....	×		
<i>Verbena hastata</i> .....	×		
<i>Erechtites hieracifolia</i> .....	×		
<i>Juncus effusus</i> .....		×	×
			more abundant
<b>Animals</b>			
<i>Totanus flavipes</i> (migrant).....	×		
<i>Totanus melanoleucus</i> (migrant).....	×		
<i>Pisobia minutilla</i> (migrant).....	×		
<i>Oxyechus vociferus</i> (migrant).....	×		
<i>Actitis macularia</i> (migrant).....	×		
<i>Ereunetes pusillus</i> (migrant).....	×		
<i>Rana clamitans</i> .....	×	×	×
<i>Rana pipiens</i> .....	×	×	×
<i>Chrysemys picta</i> .....	×	×	×
<i>Bufo americanus</i> .....	×		
<i>Umbra limi</i> .....		×	
<i>Esox vermiculatus</i> .....		×	
<i>Ondatra zibethica</i> .....		×	×
<i>Agelaius phoeniceus</i> .....		×	×
<i>Telmatodytes palustris</i> .....			×
<i>Geothlypis trichas</i> .....			×
<i>Melospiza georgiana</i> .....			×

\* In order of appearance.

## Composition of Biotic Communities

## METHODS OF STUDY

The three areas, Mentor Marsh, Lake Kelso, and Aurora Pond, described, were chosen for intensive study over the period from 1931 to 1937 inclusive, and certain phases of the study were continued at Aurora Pond through 1939.

The occurrence of all vertebrate animal life were recorded on maps of the study areas during each visit.

Fish populations were determined by seining and by observation of the catches of fishermen.

The breeding bird populations (Table 6) were worked out in the manner described by Williams (1936) by transposing all of the occurrence records for any one species taken on individual trips during the breeding season onto a single map. Closely grouped records were taken to indicate the presence of a breeding territory. Wherever possible nests were actually found for verification.

The small mammal populations (Table 7) were worked out by quadrat trapping in the same manner as did Williams (1936) except that several different sized quadrats were used; 10 meters, 15 meters, 30 meters, and 45 meters to the side. However, only the results of the first three nights trapping in 45 meter ( $\frac{1}{2}$  acre) quadrats are used in estimating populations here, although trapping results obtained from the smaller quadrats, as well as in the transects, are considered of value in the estimation of relative abundance of species. Yields of the first three nights of trapping are considered by Bole (1939) as a more accurate indication of population than longer stands. In the same investigation Bole also determined that  $\frac{1}{2}$  acre quadrats are the smallest that will give a reasonably accurate cross section of the total mammal population.

Plant abundance was studied by the quadrat method, using the same quadrats employed for the small mammal trapping. Supplementary notes were taken on field observations of abundance, dominance, competition, aspect, and other points of ecological significance. The ecological classification of plants in Table 8 is based on these data.

Since full scientific names for all plants and animals are given in Table 8, only the common names are used in Tables 6 and 7 on abundance.

TABLE 5.—Classification of Hydrarch Communities of Northeastern Ohio\* in Order of Succession.

Stage	Prisere		Subsere
	Bog type	Swamp type	
Floating plant	<i>Nymphaea advena</i> Consocias	<i>Nymphaea advena</i> Consocias	<i>Nymphaea advena</i> Consocias
Emergent vegetation	Absent	Decodon-Typha Associas	Juncus-Scirpus Associas
Heath	<i>Chamaedaphne calyculata</i> Consocias	Absent	Absent
High shrub	<i>Nemopanthus-Alnus</i> Associas	<i>Cephalanthus-Alnus</i> Associas	<i>Cornus-Rosa-Spiraea</i> Associas
Subclimax forest	<i>Larix-Acer-Betula</i> Associas	<i>Acer-Ulmus-Fraxinus</i> Associas	<i>Salix-Populus-Quercus</i> Associas
Climax forest	<i>Pinus-Tsuga</i> Association	<i>Fagus-Acer</i> Association	<i>Fagus-Acer</i> Association

\* Exclusive of flood plain sere.

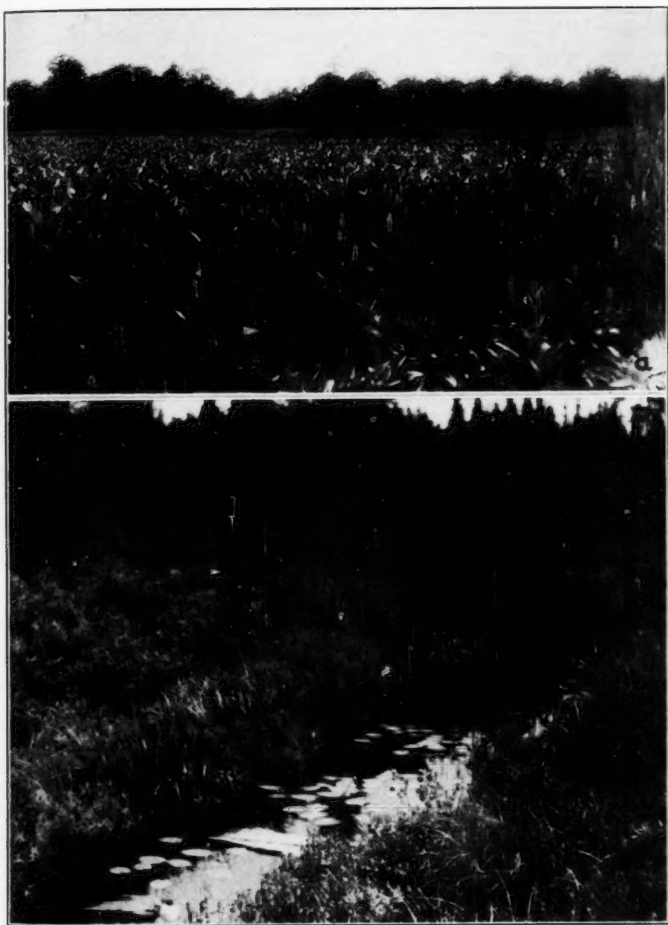


Fig. 12. Comparison of Swamp and Bog. a, Typical swamp of the Beech-Maple Association region at Aurora Pond, Ohio, showing stages from pond lily through swamp loosestrife and swamp shrub to deciduous swamp forest of elm, ash and maple. (Photo by A. B. Williams.) b, Typical bog of the Pine-Hemlock Association region at Timagami, Ontario, showing stages from pond lily through bog heath to coniferous bog forest of black spruce and tamarack.



## CLASSIFICATION OF HYDRARCH STAGES

For a better understanding of the composition of hydrarch communities, an attempt is here made to classify them on the basis of the various heretofore mentioned biotic, climatic, physiographic, and disturbing factors. In this classification (Table 5) an attempt has been made to distinguish between the typically *bog* associes (Fig. 12b), which represent boreal relics, and typically *swamp* associes (Fig. 12a), which represent the present climatic type. The *Juncus-Scirpus* and *Salix-Populus-Quercus* associes, are in the writer's opinion, characteristic of secondary succession and are seldom found in purely primary succession in northeastern Ohio. Their presence in the region at the time of the white man's arrival is not proof of their primary nature unless the possibility of secondary succession as the result of Indian or beaver activity or denudation by severe physiographic forces is eliminated.

Each one of the associes in Table 5 has various facies often depending upon the amount of intergradation between bog and swamp condition. Associes of the subsere seem to show more faciation than those of the prisere, and the type of facies is usually an indicator of the nature of the denudation.

## BOG SERE

*Nymphaea advena* Consocias (Fig. 13). — The large yellow waterlily (*Nymphaea advena*) is certainly of overwhelming influence in the floating



Fig. 13. *Nymphaea advena* Consocias. Pond-lily Zone at Aurora Pond.

plant stage in northeastern Ohio, as it is also in the Pine-Hemlock climax region to the north in Ontario, sharing the position of primary dominant with no other plant. The white waterlilies, *Castalia odorata* and *C. tuberosa* are present rarely but never in the dense, solid stands of the yellow-flowered species. The yellow waterlily raises its leaves above the water and so increases its effectiveness as a dominant species, since it affords cover for grebes, ducks, gallinules, and other life that spends more or less of its time on the surface of the water.

The substratum is comparatively firm due to the presence of the large tuberous roots of the waterlily which form a rather solid platform over the soft oozy soil.

*Chamaedaphne calyculata* Consociates (Fig. 14).—This is probably the most clearly marked and best preserved of any of the relic bog communities in northeastern Ohio, where it forms a well defined heath zone. In species composition it is very similar to the bog heath stage (Fig. 12) of the typical *Pinus-Tsuga* association, as it occurs in the Timagami region of Ontario.

In typical pine-hemlock climax bog succession of Ontario and northern Michigan a "sedge mat" or *Carex-Carex* associates forms the emergent stage that is followed by the bog heath. However, in northeastern Ohio this associates no longer exists, having been completely replaced in climatic succession by the corresponding swamp community, the *Decodon-Typha* associates that is now the mat-former in this region. Indeed peat borings at Fern Lake by Gersbacher (1939) show no *Carex* peat layer at the lower levels, indicating that probably a *Carex-Carex* associates never existed there. Wherever the bog-heath zone exists in northeastern Ohio it is completely dominated by leather leaf.

The substratum of the *Chamaedaphne calyculata* Consociates at Lake Kelso, although somewhat firmer than that of a *Carex-Carex* community, is still decidedly mat-like and shakes underfoot. It is characteristic of peat moss (*Sphagnum* sp.), which is by far the principal subdominant of this community, to climb up over and engulf the stems of the leather-leaf. The latter, however, seems to be successful in keeping its crown above the moss by continual growth. It is usually possible to trace the stems of the leather-leaf for some distance under the peat moss. This constant building up of peat moss reinforced by roots and stems of leatherleaf tends to create a firmer, higher, and dryer substratum for the occupation of the high shrub and tree stages which eventually succeed the heath.

*Nemopanthus-Alnus* Associates (Fig. 15).—In northeastern Ohio, wherever this community has developed by biotic succession directly following the *Chamaedaphne calyculata* consociates, the primary dominants are usually the tall shrubs mountain-holly (*Nemopanthus mucronata*) and hoary alder (*Alnus incana*). Occasionally, as around Fern Lake in the Lake Kelso area the much lower shrub, black huckleberry, forms a well marked *Gaylussacia baccata* facies of the *Nemopanthus-Alnus* associates. Indeed the huckleberry seems to form a transition from the low bog heath, leatherleaf, to the tall

mountain-holly and hoary alder community. Around Lake Kelso in the same area, however, there is no such intermediate stage, the leatherleaf intergrading directly with the tall bog shrubs over a comparatively wide zone (Fig. 8).

In secondary succession after destruction of bog forest, if the peat soil is not destroyed or the ground water table disturbed, bog shrubs come in almost

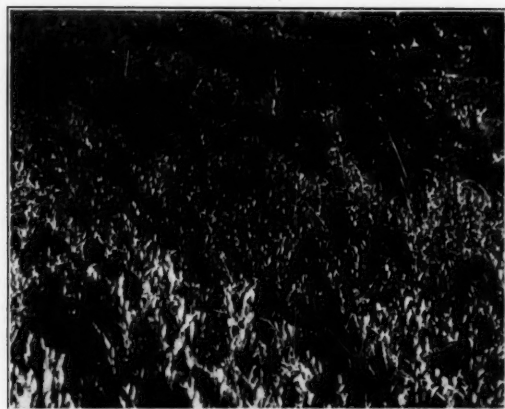


Fig. 14. *Chamaedaphne calyculata* Consociates at Fern Lake. Leatherleaf zone with members of high bog shrub zone (mountain holly and tall blueberry) in the background at right.

immediately, both from seeds and sprouts from the roots of the subdominant species of the previous bog forest. The resulting community may represent any one of a number of facies of the *Nemopanthus-Alnus* associates, in which black choke-berry, purple choke-berry, tall blueberry, poison sumac, and witherod, as well as mountain-holly and hoary alder occur in varying combinations as primary dominants.

The substratum of the tall shrub stage of bog succession is usually much firmer than that of the heath, although, where the community is the result of primary succession, the soil is constantly saturated with water. The soil of secondary succession shrub communities, however, may become fairly dry during the summer.

✧ *Larix-Acer-Betula* Associates (Fig. 16).—The subclimax forest stage of the bog sere in northeastern Ohio is most characteristically dominated by the tamarack (*Larix laricina*), red maple (*Acer rubrum*), and yellow birch (*Betula lutea*), forming a community which evidently represents the *Larix-Thuja* associates characteristic of the true *Pinus-Tsuga* association hydrarch succession. The community in northeastern Ohio has suffered severely from the hand of man due to the comparatively high commercial value of the tamarack,

and the depredations of the larch sawfly. In many places where tamarack formerly occurred, at the present time it is lacking, leaving only the red maple and yellow birch as primary dominants. For some reason, possibly due to a soil acidity factor, the white cedar (*Thuja occidentalis*) is not represented at all in the bog forests of northeastern Ohio, although present in primary dominant capacity in certain bogs of the limestone area of the western part of the State.



Fig. 15. *Nemopanthus-Alnus* Associates at Lake Kelso, showing chiefly hoary alder.

Secondary dominants of the *Larix-Acer-Betula* associates, such as black cherry, white elm, black ash, or tupelo, become numerous enough in certain areas to replace the tamarack, yellow birch, or red maple, as primary dominants and to form various facies. Some of these facies might be considered as representing the *Acer-Ulmus-Fraxinus* associates of the swamp succession were it not for the subdominant species, which are more characteristic of the boreal hydrosere. These facies undoubtedly represent stages of climatic succession to the swamp sere community usually appearing as the result of secondary succession.

The substratum of this associates is a firm woody peat. At the surface it is almost a solid mass of roots of the trees and other plants of the community.

In the winter and early spring several inches of water usually overlie the peat, but in the summer and autumn the ground water level may be a considerable distance below the surface and the peat may become rather dry, although from 1937 to 1939 the peat remained very wet all summer. In exceptionally dry seasons there is danger of this peat catching fire, as happened at Aurora Pond in the autumn of 1933.



Fig. 16. *Larix-Acer-Betula* Associes. a, Summer aspect showing red maple, hemlock and cinnamon fern in the foreground at Aurora Pond. (Photo by A. B. Williams.) b, Winter aspect showing red maples and yellow birch at Lake Kelso. (Photo by A. B. Williams.)

#### SWAMP SERE

*Nymphaea advena Consociet* (Fig. 13). — The floating plant stage of swamp succession differs so little in either plant or animal composition from the corresponding stage of bog succession that it is not practical to consider it as a distinct associes. The large yellow waterlily is equally dominant in the floating plant stage leading up to typical swamp shrub and swamp forest communities as it is in a succession of bog communities. The wide ranging *Nymphaea advena* probably represents in northeastern Ohio a *Nymphaea-Nelumbo* associes of more southern distribution with which the tuberous waterlily *Castalia tuberosa* is also commonly associated.

*Decodon-Typha* Associes (Fig. 17). — There are two distinct types of communities representing the emerging stage: (1) a floating mat usually dominated almost completely by swamp loosestrife (*Decodon verticillata*) and similar to the "sedge mat" of the boreal hydrosere; (2) a marsh in which broad-leaf cat-tail (*Typha latifolia*) is usually the primary dominant. The type that occurs depends upon the topography and the physiographic conditions of that particular area.

TABLE 6.—Breeding Bird Populations. Average\* Number of Pairs per 100 Acres (40 hectares) for Each Community.

Species	Juncus- Scirpus Associates	Cephalanthus- Alnus Associates	Larix- Acer-Betula Associates
Redwinged blackbird .....	113	144	
Prairie marsh wren .....	78	3	
Swamp sparrow .....	68	49	4
Virginia rail .....	22		
Least bittern .....	12		
Short-billed marsh wren .....	10		
Song sparrow .....	8	49	12
Florida gallinule .....	5		
Sora .....	3		
Mallard .....	3		
Killdeer .....	1		
Yellow warbler .....		80	
Alder flycatcher .....		80	
Catbird .....		31	4
Yellowthroat .....		28	13
Kingbird .....		24	
Goldfinch .....		21	
Tree swallow .....		7	
Green heron .....		7	1
Robin .....		3	4
Red-eyed vireo .....			9
Black-capped chickadee .....			9
Grinnell waterthrush .....			9
House wren .....			7
Ovenbird .....			7
Downy woodpecker .....			7
Wood pewee .....			5
Tufted titmouse .....			4
White-breasted nuthatch .....			4
Blue Jay .....			3
Rose-breasted grosbeak .....			2
Crow .....			2
Scarlet tanager .....			2
Flicker .....			2
Crested flycatcher .....			2
Cardinal .....			1
Wood thrush .....			1
Wilson thrush .....			1
Hairy woodpecker .....			1
Black-billed cuckoo .....			1
Red-shouldered hawk .....			1
Bluebird .....			1
Cowbird .....			1
Prothonotary warbler .....			1
Totals .....	323	526	121

\* Based on 7 nesting seasons.

TABLE 7.—Small Mammal Populations, Average\* Number Per Acre (0.4 hectares) for Each Community.

Species	Juncus-Scirpus Associates	Cephalanthus-Alnus Associates	Acer-Ulmus-Fraxinus Associates	Larix-Acer-Betula Associates
Meadow vole .....	23	5	11	6
Northern deer mouse .....	1	9	13	8
House mouse .....	2		1	
Hudson Bay jumping mouse.....		1		1
Short-tailed shrew .....	2	21	6	9
Canada shrew .....	2	12	5	5
Smoky shrew .....	3			3
Star-nosed mole .....	1			2
Hairy-tailed mole .....	1	1		
Eastern chipmunk .....		1		2
Small eastern flying squirrel.....		1	2	1
Mississippi Valley fox squirrel.....		1		
Red squirrel .....		1		2
Totals .....	35	53	38	39

\* Based on 3 quadrats for each community trapped in 3 separate years.

The cat-tail is characteristic of the emerging stage chiefly in the Lake Erie shore and delta marshes, where the shore rises very gradually and the community is subjected to the extreme physiographic forces of storms, floods, and seiches. However, no extensive cat-tail marshes such as are found at the west end of Lake Erie occur in the northeastern Ohio area. Where the cat-tail occurs with swamp loosestrife it is usually at the mouths of inflowing streams where silting is comparatively heavy or in areas around muskrat houses, where the substratum, a soft muck usually more or less heavily infiltrated with mineral silts, is constantly being churned up by these mammals.

Where physiographic conditions are not severe and the community has not been interfered with, as in Norton's Pond in Mentor Marsh, and at Lake Kelso, the swamp loosestrife, in an almost pure stand, forms a remarkably well defined zone. The function of the swamp loosestrife like that of sedges in bog succession is to form on the water a flimsy mat of vegetable debris held together by roots which eventually become stable enough for other plants to invade. Cat-tail is not a mat-former and for that reason depends upon swamp loosestrife or silting by water currents to build up a substratum suitable for its invasion. Cat-tail is admirably adapted to secondary succession and invasion of bare areas denuded by floods or other physiographic forces because it becomes established quickly and spreads rapidly in a denuded area where the water is not too deep for its growth. If left undisturbed, however, it will eventually be entirely replaced by swamp loosestrife.

*Juncus-Scirpus Associates* (Fig. 18). — This community apparently corresponds to the sedge meadow stage of other authors, including Weaver and Clements (1929, p. 58). In northeastern Ohio, however, it is almost certain that the stage does not exist except in secondary succession on a substratum





Fig. 17. *Decodon-Typha* Associates. The outer edge of the Swamp Loosestrife-Cat-tail zone where it comes in contact with the yellow water-lily zone at Aurora Pond.

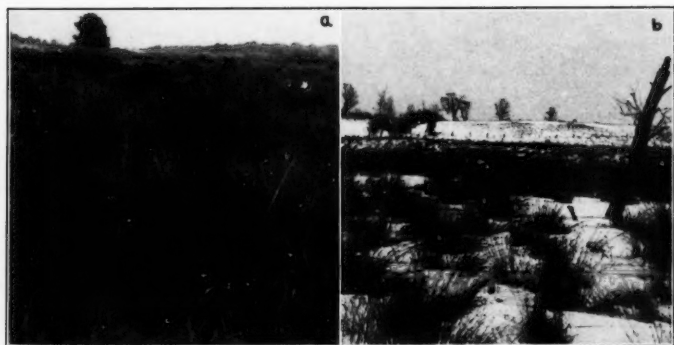


Fig. 18. *Juncus-Scirpus* Associates at Aurora Pond. a, Late summer aspect of sedge meadow at Station 1, showing the numerous grasses and herbs growing with the *Juncus* and *Scirpus*. b, Winter aspect in same area showing the stiff stalks of the *Juncus* to be almost the only standing vegetation.

that is already suitable for the establishment of a shrub or forest community. In wetter situations a cat-tail or a bur-reed community similar to that of primary succession develops immediately. After denudation of swamp shrub or swamp forest or flooding of grassland the rapidly growing rushes, grasses, and sedges characteristic of the "sedge meadow" quickly become established, resulting in one or another of the many facies of the *Juncus-Scirpus* Associates. Within a few years, however, if no further interference occurs swamp shrub replaces the meadow. A good example of this process is taking place at Aurora Pond (Fig. 11). Nowhere in northeastern Ohio has this community been found forming a definite stage in what is considered definitely primary succession.

The *Juncus-Scirpus* associates is very commonly encountered in northeastern Ohio, where swamp forest and swamp shrub have been cleared and the land kept open for grazing which is the only type of agricultural use to which such land can be put without artificial draining. The associates occurs in many facies, most of which include common rush (*Juncus effusus*), or wool-grass (*Scirpus cyperinus*), or both, among their primary dominants. Rice cut-grass (*Homalocenchrus oryzoides*) is almost invariably present in great abundance frequently exerting much greater dominance than either the common rush or wool-grass. Its dominance is distinctly more seasonal than either of the other two species; however common rush, being more "woody" and more or less evergreen in nature, probably exerts more influence in the winter and spring before the other plants have come up. At such times it frequently forms the only standing cover in the community (Fig. 18), and is used extensively for nesting sites by early nesting birds of this community, such as the redwinged blackbird, prairie marsh wren, swamp sparrow, and Virginia rail. At that time of year there is always some standing water in the community and the hummocks formed by the clumps of common rush afford favorite retreats for the meadow vole and Canada shrew, and are used as resting places by the muskrat. By the middle of the summer the water has receded from the surface of the substratum and wool-grass, rice cut-grass, and many herbaceous plants, have grown up and overtopped the common rush, and from then on until the end of the growing season its importance in the community is minimized. Prairie marsh wrens, redwinged blackbirds, and swamp sparrows, use other plants for their later brood nests; and meadow voles, Canada shrews, and Hudson Bay jumping mice can spread out over the entire area and use the new vegetation for cover.

The *Juncus-Scirpus* associates adjacent to Aurora Pond is the spawning place for many carp, black bullheads and frogs of various species. The eggs of these animals must hatch and the young leave the area or (in the case of frogs) metamorphose before the water recedes from the surface as usually happens early in the summer. This is a community of very marked seasonal aspection in both its plant and animal life.

The substratum of the *Juncus-Scirpus* associates varies greatly not only in its water content seasonally but in the composition of its soil, depending upon

the nature of the community occupying the situation previous to denudation. In the experimental area (Station 1) at Aurora Pond, where the marsh was originally created by flooding a pasture, the soil is blue clay overlaid with a few inches of muck formed from the mixture of clay with the more or less decomposed marsh vegetation.

*Cephalanthus-Alnus* Associates (Fig. 19).—In primary succession the swamp shrub stage in northeastern Ohio has buttonbush (*Cephalanthus occidentalis*) or smooth alder (*Alnus rugosa*) or both as primary dominant species. The substratum is usually a soft oozy peat difficult to walk on except where the roots of the shrubs have formed a frail platform. The soil is covered with water except during the summer and autumn and even then the water seldom gets more than a few centimeters below the surface.

*Cornus-Rosa-Spiraea* Associates (Fig. 20).—This is the representative of the shrub stage in secondary succession. It comes in rapidly after destruction of swamp forest by fire or cutting, frequently without a preliminary development of the *Juncus-Scirpus* associates. It is apt to appear rather quickly in the dryer



Fig. 19. *Cephalanthus-Alnus* Associates at Mentor Marsh, showing chiefly buttonbush.

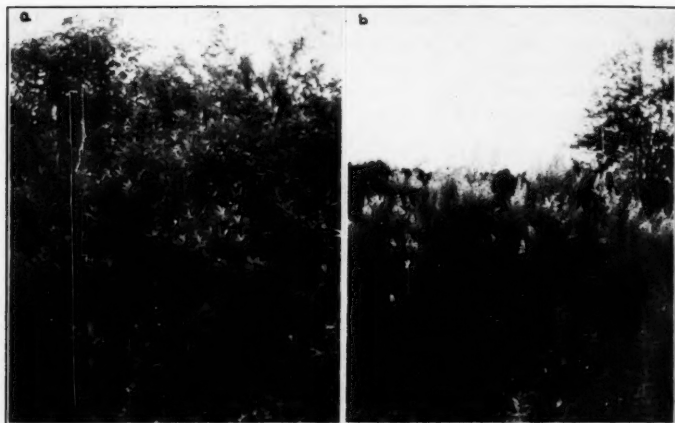


Fig. 20. *Cornus-Rosa-Spiraea* Associates at Aurora Pond. a, View of community in which swamp rose dominates. b, View of community in which meadowsweet dominates. (Photo by A. B. Williams.)

portions of a *Juncus-Scirpus* meadow, while buttonbush, representing the primary succession *Cephalanthus-Alnus* associates, develops more slowly in the wetter portions.

The most usual primary dominants in this rather heterogeneous associates are red-osier dogwood (*Cornus stolonifera*), swamp rose (*Rosa carolina*), and meadowsweet (*Spiraea alba*), but other shrubs such as other dogwoods and elderberry (*Sambucus canadensis*) frequently play very important parts.

*Salix-Populus-Quercus* Associates.—This rather broad grouping encompasses all of the apparently secondary succession swamp forest types in a single associates. These are usually characterized by the abundance of some species of willow, poplar or oak. The writer considers it very doubtful that any species of willow or poplar occurs as a primary dominant species in primary succession in northeastern Ohio. It is likely that the so-called willow-poplar stage, recognized by Sampson (1930) as the first stage of the swamp forest in northern Ohio, represents secondary succession, at least in the northeastern part of the State. The writer has been unable to recognize a willow-poplar community in any swamp sere which seemed definitely to be primary in nature. This is also true of swamp forests of oak (*Quercus bicolor* and *Quercus palustris*), with the exception of a few cases on the Lake Plain, where apparently primary succession forests of swamp white oak and pin oak similar to those characteristic of succession to the oak-hickory climax are found. These exceptions might be considered as relics of a former dryer period or as resulting from

local physiographic conditions. It is understood that the flood plain sere is considered distinct from swamp succession, and is, therefore, omitted from this discussion. The *Salix-Populus-Quercus* associates is, therefore, to be considered as occurring normally in secondary succession in northeastern Ohio, and is very commonly met with in that region.

*Acer-Ulmus-Fraxinus Associates* (Fig. 21). — This is the swamp forest of the true climatic prisere of northeastern Ohio commonly mentioned in the literature as characteristic of the deciduous forest region of northeastern North America. In the area covered by this report the red maple (*Acer rubrum*), silver maple (*Acer saccharinum*), white elm (*Ulmus americana*), black ash (*Fraxinus nigra*), white ash (*Fraxinus americana*), swamp white oak (*Quercus*



Fig. 21. *Acer-Ulmus-Fraxinus Associates* at Mentor Marsh. Dense ground cover of Royal Fern, Sensitive Fern and Lizard's Tail visible in the foreground.

*bicolor*), and pin oak (*Quercus palustris*), are the primary dominants. Sampson (1930) has adequately treated this community with respect to the major aspects of its tree composition. The presence of the black ash as a primary dominant should probably be considered as an indication of intergradation between bog and typical swamp conditions, although the species is frequently present in swamp forests of otherwise non-boreal aspect. The black ash is also a characteristic tree of bog succession farther north, and it is replaced by white and other species of ash farther south.

There are numerous slightly differentiated communities which in some cases are transitional between the *Acer-Ulmus-Fraxinus* associates and the *Fagus-Acer* association. Some of these facies and transitional stages have been described by various authors, including Sampson (1930) and Hicks (1933). Among the most commonly recognized of these are the red maple-white elm-white ash, burr oak-butternut hickory, and red maple-white elm facies; the red oak-linden, tulip-walnut, and beech-red maple ecotones.

The substratum of the *Acer-Ulmus-Fraxinus* Associates is composed of firmly packed peat, particularly on the surface where it is firmly held together by the roots of trees and lesser plants. Although flooded with water in the winter and spring, during the summer the peat frequently becomes exceedingly dry.

#### ECOLOGICAL CLASSIFICATION OF SPECIES

The ecologically more important species of plant and vertebrate animal life of the above described stages of swamp and bog succession are listed in Table 8, with symbols indicating their ecological position in the various communities.

The identification of most of the forms, as well as a great many more not listed here, has been made from specimens by specialists in the systematics of the various groups involved, and the nomenclature is that used by them. The vascular plants were identified by Professor John H. Schaffner, the fish by Milton B. Trautman, the amphibians by Dr. Charles F. Walker, the reptiles by Roger Conant, the mammals by B. P. Bole, Jr., and the birds by the writer. All specimens are deposited in the collections of the Cleveland Museum of Natural History.

There is little doubt that many of the species, particularly of the more mobile animals, occur in more communities than is indicated by Table 8. However, when the writer has had no direct evidence of this they are omitted from the community. Unless otherwise indicated seasonal member birds are included only on the basis of occurrence during the breeding season, at which time they are of greatest influence in the community. A few of particular importance in winter are included however.

TABLE 8.—Ecological Classification of Northeastern Ohio Hydrarch Species.

Symbols: PD—Primary dominant; SD—Secondary dominant; SUB—Subdominant;  
 PP—Permanent predominant; SP—Seasonal predominant; SM—Seasonal  
 member; PM—Permanent member.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prisiere)	<i>Decodon-Typha</i> Associates (Swamp prisiere)	<i>Juncus-Scirpus</i> Associates (Swamp subaere)	<i>Chamaedaphne calyculata</i> Consociates (Bog prisiere)	<i>Nemopanthus-Alnus</i> Associates (Bog prisiere)	<i>Cephalanthus-Alnus</i> Associates (Swamp prisiere)	<i>Larix-Acer-Betula</i> Associates (Bog prisiere)	<i>Acer-Ulmus-Fraxinus</i> Associates (Swamp prisiere)
PLANTS								
Peat moss								
<i>Sphagnum</i> sp. ....				SUB	SUB		SUB	
Royal fern								
<i>Osmunda regalis</i> .....				SUB	SUB	SUB	SUB	SUB
Cinnamon fern								
<i>Osmunda cinnamomea</i>					SUB	SUB	SUB	SUB
Marsh shield fern								
<i>Dryopteris thelypteris</i>		SUB	SUB	SUB	SUB	SUB	SUB	
Spinulose shield fern								
<i>Dryopteris spinulosa</i> ....							SUB	
Sensitive fern								
<i>Onoclea sensibilis</i> .....			SUB			SUB	SUB	SUB
Hemlock								
<i>Tsuga canadensis</i> .....							SD	
Tamarack								
<i>Larix laricina</i> .....				SD	SD		PD	
White pine								
<i>Pinus strobus</i> .....							SD	
Broad-leaf arrow-head								
<i>Sagittaria latifolia</i> .....		SUB	SD	SUB		SUB		
Common floating pondweed								
<i>Potamogeton natans</i> .....	SD							
Long-leaf pondweed								
<i>Potamogeton americanus</i>	SD							
Nuttall's pondweed								
<i>Potamogeton epihydrus</i>	SD							
Slender naias								
<i>Naias flexilis</i> .....	SUB							
Large yellow water lily								
<i>Nymphaea advena</i> .....	PD	SUB						
Common water weed								
<i>Philotria canadensis</i> .....	SUB							
Broad-fruited bur reed								
<i>Sparganium eurycarpum</i>		PD	SD					
Broad-leaf cat-tail								
<i>Typha latifolia</i> .....		PD	SD	SUB				
Sweet flag								
<i>Acorus calamus</i> .....		SD	SD					



TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prairie)	Decodon-Typha Associates (Swamp prairie)	Juncus-Scirpus Associates (Swamp subere)	<i>Chamaedaphne calyculata</i> Consociates (Bog prairie)	Nemopanthus-Alnus Associates (Bog prairie)	Cephalanthus-Alnus Associates (Swamp prairie)	Larix-Acer-Betula Associates (Bog prairie)	Acer-Ulmus-Fraxinus Associates (Swamp prairie)
Skunk cabbage <i>Spathyema foetida</i> .....					SUB	SUB	SUB	SUB
Lesser duckweed <i>Lemna minor</i> .....	SUB	SUB	SUB					
Wool grass <i>Scirpus cyperinus</i> .....		SD	PD					
Great bulrush <i>Scirpus validus</i> .....		SD	SD					
Virginia cotton sedge <i>Eriophorum virginicum</i> .....				SUB				
Blunt spike rush <i>Eleocharis obtusa</i> .....		SUB	SD			SUB		
Dulichium <i>Dulichium arundinaceum</i> .....			SD	SUB				
Red-rooted cyperus <i>Cyperus erythrorhizos</i> .....			SD					
White beak rush <i>Rhynchospora alba</i> .....				SUB				
Fox sedge <i>Carex vulpinoidea</i> .....			SD					
Pointed broom sedge <i>Carex scoparia</i> .....			SD	SUB				
Fringed sedge <i>Carex crinita</i> .....			SD				SUB	
Bristly sedge <i>Carex comosa</i> .....			SD					
Hop sedge <i>Carex lupulina</i> .....			SD				SUB	
Common reed grass <i>Phragmites phragmites</i> .....		SD						
Rice cut-grass <i>Homalocenchrus oryzoides</i> .....			PD			SUB		
False lily-of-the-valley <i>Unifolium canadense</i> .....							SUB	
Pickering weed <i>Pontederia cordata</i> .....	SD	SUB						
Common rush <i>Juncus effusus</i> .....		SD	PD	SUB		SUB		
Goldthread <i>Coptis trifolia</i> .....							SUB	
Marsh marigold <i>Caltha palustris</i> .....							SUB	
Hornleaf <i>Ceratophyllum demersum</i> .....	SUB						SUB	
Spicebush								

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prisiere)	<i>Decodon-Typha</i> Associates (Swamp prisiere)	<i>Juncus-Scirpus</i> Associates (Swamp subserie)	<i>Chamaedaphne calyculata</i> Consociates (Bog prisiere)	<i>Nemopanthus-Alnus</i> Associates (Bog prisiere)	<i>Cephalanthus-Alnus</i> Associates (Swamp prisiere)	<i>Larix-Acer-Betula</i> Associates (Bog prisiere)	<i>Acer-Ulmus-Fraxinus</i> Associates (Swamp prisiere)
<i>Benzoïn aestivale</i> .....						SD	SUB	SUB
Pitcher plant								
<i>Sarracenia purpurea</i> ....				SUB				
Roundleaf sundew								
<i>Drosera rotundifolia</i> ....				SUB				
Spotted Touch-me-not								
<i>Impatiens biflora</i> .....			SUB			SUB	SUB	SUB
Swamp rose mallow								
<i>Hibiscus moscheutos</i> .....		SD						
Marsh St. John's-wort								
<i>Triadenum virginicum</i>		SUB	SUB	SUB	SUB	SUB	SUB	
Arrow-leaf tearthumb								
<i>Tracaulon sagittatum</i> ....			SD					
Halberd-leaf tearthumb								
<i>Tracaulon arifolium</i> ....						SUB		SUB
Wild smartweed								
<i>Persicaria hydropiperoides</i>		SUB	SD					
Lizard's-tail								
<i>Saururus cernuus</i> .....						SUB	SUB	SUB
Hispid dewberry								
<i>Rubus hispidus</i> .....					SUB		SUB	
Meadowsweet								
<i>Spiraea alba</i> .....					SD	SD		
Steeple-bush								
<i>Spiraea tomentosa</i> .....			SD	SD	SUB			
Swamp rose								
<i>Rosa carolina</i> .....				SD	SD	SD		
Black cherry								
<i>Prunus virginiana</i> .....							SD	SD
Purple chokeberry								
<i>Aronia atropurpurea</i> ....				SD	PD			
Black chokeberry								
<i>Aronia melanocarpa</i> ....					SD		SUB	
Common junberry								
<i>Amelanchier canadensis</i>					SD		SUB	
Swamp loosestrife								
<i>Decodon verticillatus</i> ....		PD	SD	SD		SUB		
Virginia creeper								
<i>Parthanocissus quinquefolia</i>							SUB	SUB
Mountain holly					PD		SUB	
<i>Nemopanthus mucronata</i>					PD		SUB	
Winterberry								
<i>Ilex verticillata</i> .....					SD	SD	SUB	SUB
Red maple								
<i>Acer rubrum</i> .....				SD	SD		PD	PD

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prairie)	Decodon-Typha Associates (Swamp prairie)	<i>Juncus-Scirpus</i> Associates (Swamp subprairie)	<i>Chamaedaphne calyculata</i> Consociates (Bog prairie)	<i>Nemophanthus-Alnus</i> Associates (Bog prairie)	<i>Cephalanthus-Alnus</i> Associates (Swamp prairie)	<i>Larix-Acer-Betula</i> Associates (Bog prairie)	<i>Acer-Ulmus-Fraxinus</i> Associates (Swamp prairie)
Silver maple <i>Acer saccharinum</i> .....								PD
Poison sumac <i>Toxicodendron vernix</i> ....				SD	SD	SD	SUB	SUB
Poison ivy <i>Toxicodendron radicans</i>							SUB	SUB
White elm <i>Ulmus americana</i> .....							SD	PD
False nettle <i>Boehmeria cylindrica</i>		SUB	SUB	SUB	SUB	SUB	SUB	SUB
American beech <i>Fagus grandifolia</i> .....							SD	SD
Swamp white oak <i>Quercus bicolor</i> .....							SD	PD
Pin oak <i>Quercus palustris</i> .....								PD
Yellow birch <i>Betula lutea</i> .....				SD	SD		PD	SD
Hoary alder <i>Alnus incana</i> .....					PD	SD	SUB	SUB
Smooth alder <i>Alnus rugosa</i> .....					SD	PD		SUB
Swamp poplar <i>Populus heterophylla</i> ....						SD		
American aspen <i>Populus tremuloides</i> .....					SD	SD	SD	SD
Peachleaf willow <i>Salix amygdaloides</i> .....						SD		
Black willow <i>Salix nigra</i> .....			SD			SD		SD
Pussy willow <i>Salix discolor</i> .....						SD		
Wild black currant <i>Ribes americanum</i> .....							SUB	SUB
Mermaid weed <i>Proserpinaca palustris</i>		SUB	SUB					
Leather-leaf <i>Chamaedaphne calyculata</i>				PD	SUB			
Creeping wintergreen <i>Gaultheria procumbens</i>				SUB	SUB		SUB	
Tall blueberry <i>Vaccinium corymbosum</i>					PD	SD	SUB	
Low blueberry <i>Vaccinium vacillans</i> .....				SD	SUB		SUB	

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prisiere)	<i>Decodon-Typha</i> Associates (Swamp prisiere)	<i>Juncus-Scirpus</i> Associates (Swamp subsiere)	<i>Chamaedaphne calyculata</i> Consociates (Bog prisiere)	<i>Nemopanthus-Alnus</i> Associates (Bog prisiere)	<i>Cephalanthus-Alnus</i> Associates (Swamp prisiere)	<i>Larix-Acer-Betula</i> Associates (Bog prisiere)	<i>Acer-Ulmus-Fraxinus</i> Associates (Swamp prisiere)
Dwarf blueberry <i>Vaccinium angustifolium</i>					SUB		SUB	
Large cranberry <i>Oxycoccus macrocarpus</i>				SUB				
Black huckleberry <i>Gaylussacia baccata</i> ....				SD	SUB		SUB	
Black ash <i>Fraxinus nigra</i> .....							SD	SD
White ash <i>Fraxinus americana</i> .....								PD
Buckbeam <i>Menyanthes trifoliata</i>				SUB				
Swamp milkweed <i>Asclepias incarnata</i> .....			SD					
Bitter-sweet <i>Solanum dulcamara</i> .....						SUB		
Greater bladderwort <i>Utricularia macrorhiza</i>	SUB		SUB					
Blue vervain <i>Verbena hastata</i> .....			SD					
Wild sarsaparilla <i>Aralia nudicaulis</i> .....							SUB	SUB
Silky dogwood <i>Cornus amomum</i> .....			SD			SD		
Red-osier dogwood <i>Cornus stolonifera</i> .....			SD		SD	SD	SUB	SUB
Dwarf dogwood <i>Cynoxylon canadense</i>							SUB	
Tupelo <i>Nyssa sylvatica</i> .....							SD	SD
Buttonbush <i>Cephalanthus occidentalis</i>			SD			PD		SUB
Partridge-berry <i>Mitchella repens</i> .....			SUB	SUB			SUB	
Common elderberry <i>Sambucus canadensis</i>						SD		SUB
Toothed arrow-wood <i>Viburnum dentatum</i> ....						SD	SUB	SUB
Withe-rod <i>Viburnum cassinoides</i>					SD		SUB	
Nodding bur marigold <i>Bidens cernua</i> .....			SD			SUB		
Tall tickseed <i>Bidens coronata</i> .....		SD	SD			SUB		

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prisiere)	Decodon-Typha Associates (Swamp prisiere)	Juncus-Scirpus Associates (Swamp subsiere)	<i>Chamaedaphne calyculata</i> Consociates (Bog prisiere)	Nemophanthus-Alnus Associates (Bog prisiere)	Cephalanthus-Alnus Associates (Swamp prisiere)	Larix-Acer-Betula Associates (Bog prisiere)	Acer-Ulmus-Fraxinus Associates (Swamp prisiere)
FISHES								
Carp								
<i>Cyprinus carpio</i> .....	PP	SP	SP					
Golden shiner								
<i>Notemigonus c. crysoleucas</i>	PP							
Black bullhead								
<i>Ameiurus m. melas</i> .....	PP	SP	SP					
Western mudminnow								
<i>Umbra limi</i> .....		SP	SP			SM		
Mud pickerel								
<i>Esox vermiculatus</i> .....	PM	SM	SM					
Yellow perch								
<i>Perca flavescens</i> .....	PP							
Largemouth bass								
<i>Aplites salmoides</i> .....	PM							
Bluegill								
<i>Helioperca incisor</i> .....	PP							
Common sunfish								
<i>Eupomotis gibbosus</i> .....	PP							
Rock bass								
<i>Ambloplites rupestris</i> ....	PM							
Black crappie								
<i>Pomoxis sparoides</i> .....	PP							
AMPHIBIANS								
Common newt								
<i>Triturus v. viridescens</i>	SM							
Dusky salamander								
<i>Desmognathus f. fuscus</i>					SM	SM		
American toad								
<i>Bufo americanus</i> .....		SM	SM	SM		SM		SM
Swamp tree frog								
<i>Pseudacris t. triseriata</i>		SP	SP	SM		SP		SM
Spring peeper		SP	SP			SP		SP
<i>Hyla crucifer</i> .....		SP	SP			SP		SP
Tree toad								
<i>Hyla versicolor</i> .....		SM	SM			SM		SM
Bullfrog								
<i>Rana catesbiana</i> .....	SP	SM	SM					
Green frog								
<i>Rana clamitans</i> .....		SP	SP	SM		SP	SM	SM
Pickerel frog								
<i>Rana palustris</i> .....		SM	SM			SM		SM
Leopard frog								
<i>Rana pipiens</i> .....		SP	SP			SP		SM

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prairie)	<i>Decodon-Typha</i> Associates (Swamp prairie)	<i>Juncus-Scirpus</i> Associates (Swamp subere)	<i>Chamaedaphne calyculata</i> Consociates (Bog prairie)	<i>Nemopanthus-Alnus</i> Associates (Bog prairie)	<i>Cephalanthus-Alnus</i> Associates (Swamp prairie)	<i>Larix-Acer-Betula</i> Associates (Bog prairie)	<i>Acer-Ulmus-Fraxinus</i> Associates (Swamp prairie)
Wood frog <i>Rana s. sylvatica</i> .....		SP	SP			SP		SP
REPTILES								
Queen snake <i>Natrix septemvittata</i> ....		SM	SM			SM		
Common water snake <i>Natrix s. sipedon</i> .....	SM	SP	SP	SM		SP		
DeKay Snake <i>Storeria dekayi</i> .....		SM	SM	SM		SM	SM	SM
Ribbon snake <i>Thamnophis s. sauritus</i>		SP	SP		SM	SP	SM	SM
Common garter snake <i>Thamnophis s. sirtalis</i>			SP		SM	SP	SM	SM
Musk turtle <i>Sternotherus odoratus</i> ....	SM							
Common snapping turtle <i>Chelydra serpentina</i> ....	SM	SM	SM					
Spotted turtle <i>Clemmys guttata</i> .....	SM	SM	SM	SM				
Blanding turtle <i>Emys blandingii</i> .....	SM	SM				SM		
Western painted turtle <i>Chrysemys picta marginata</i>	SP	SP	SP	SM				
BIRDS								
Pied-billed grebe <i>Podilymbus p. podiceps</i>	SM	SM	SM					
Eastern green heron <i>Butorides v. virescens</i> ....					SM	SM		
American bittern <i>Botaurus lentiginosus</i> ....		SM				SM		
Eastern least bittern <i>Ixobrychus c. exilis</i> .....		SM	SM					
Common mallard <i>Anas p. platyrhynchos</i> ....	SM	SM	SM					
Common black duck <i>Anas rubripes tristis</i> ....	SM	SM	SM				SM	
Blue-winged teal <i>Querquedula discors</i> ....	SM	SM	SM					
Wood duck <i>Aix sponsa</i> .....	SM	SM	SM					
Marsh hawk <i>Circus cyaneus hudsonius</i>			SM			SM		
Appalachian ruffed grouse <i>Bonasa u. monticola</i> ....								PM

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prisiere)	Decodon-Typha Asociates (Swamp prisiere)	Juncus-Scirpus Asociates (Swamp subsiere)	<i>Chamaedaphne calyculata</i> Consociates (Bog prisiere)	Nemopanthus-Alnus Asociates (Bog prisiere)	Cephalanthus-Alnus Asociates (Swamp prisiere)	Larix-Acer-Betula Asociates (Bog prisiere)	Acer-Ulmus-Fraxinus Asociates (Swamp prisiere)
Eastern bobwhite <i>Colinus v. virginianus</i> ....			SM winter			SM winter		
Ring-necked pheasant <i>Phasianus colchicus</i> <i>torquatus</i> .....			SM winter			SM winter		
Virginia rail <i>Rallus l. limicola</i> .....		SP	SP			SM		
Sora <i>Porzana carolina</i> .....		SM	SM			SM		
Florida gallinule <i>Callinula</i> <i>chloropus cachinnans</i> ....		SM	SM			SM		
Northern barred owl <i>Strix v. varia</i> .....							PM	PM
Northern flicker <i>Colaptes auratus luteus</i>					SM	SM	SM	SM
Northern pileated wood- pecker <i>Phloeotomus</i> <i>pileatus abieticola</i> ....							PM	
Yellow-bellied sapsucker <i>Sphyrapicus v. varius</i> ....							SM	
Eastern hairy woodpecker <i>Dryobates v. villosus</i> ....					PM	PM	PM	PM
North. downy woodpecker <i>Dryobates pubescens</i> <i>medianus</i> .....					PM	PM	PP	PP
Eastern kingbird <i>Tyrannus t. tyrannus</i> ....						SP		
Northern crested flycatcher <i>Myiarchus crinitus boreus</i>							SM	SM
Alder flycatcher <i>Empidonax t. traillii</i> ....					SM	SP		
Eastern wood pewee <i>Horizopus v. virens</i> ....							SP	SP
Tree swallow <i>Iridoprocne b. bicolor</i> ....						SM		
Northern blue jay <i>Cyanocitta cristata bromia</i>							PM	PM
Eastern crow <i>Corvus b. brachyrhynchos</i>							SM	SM
Black-capped chickadee <i>Penthestes a. atricapillus</i>					PM	PM	PP	PP
Tufted titmouse <i>Baeolophus bicolor</i> ....							PM	PP



TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prairie)	<i>Decodon-Typha</i> Associates (Swamp prairie)	<i>Juncus-Scirpus</i> Associates (Swamp subere)	<i>Chamaedaphne calyculata</i> Consociates (Bog prairie)	<i>Nemopanthus-Alnus</i> Associates (Bog prairie)	<i>Cephalanthus-Alnus</i> Associates (Swamp prairie)	<i>Larix-Acer-Betula</i> Associates (Bog prairie)	<i>Acer-Ulmus-Fraxinus</i> Associates (Swamp prairie)
White-breasted nuthatch <i>Sitta carolinensis cooki</i>							PM	PP
Ohio house wren <i>Troglodytes aedon baldwini</i>					SM	SM	SM	SM
Short-billed marsh wren <i>Cistothorus stellaris</i> .....			SP					
Catbird <i>Dumetella carolinensis</i>					SP	SP	SM	SM
Eastern robin <i>Turdus m. migratorius</i>						SM	SM	SM
Wilson thrush <i>Hylochichla f. fuscescens</i>					SM		SM	
Red-eyed vireo <i>Vireosylva olivacea</i>							SP	SP
Eastern yellow warbler <i>Dendroica petechia aestiva</i>					SP	SP		
Magnolia warbler <i>Dendroica magnolia</i> .....							SM	
Black-throated green warbler <i>Dendroica v. virens</i> .....							SM	
Blackburnian warbler <i>Dendroica fusca</i> .....							SM	
Chestnut-sided warbler <i>Dendroica pensylvanica</i>					SM	SM		
Eastern ovenbird <i>Seiurus a. aurocapillus</i> ....							SP	SP
Grinnell waterthrush <i>Seiurus noveboracensis</i> <i>notabilis</i> .....							SP	
Northern yellowthroat <i>Geothlypis trichas</i> <i>brachidactyla</i> .....				SP	SP	SP	SP	SP
Canada warbler <i>Wilsonia canadensis</i> ....							SM	
American redstart <i>Setophaga r. ruticilla</i> ....							SM	SM
East. red-winged blackbird <i>Agelaius p. phoeniceus</i>		SP	SP			SP		
Scarlet tanager <i>Piranga olivacea</i> .....							SM	SM
Eastern cardinal <i>Richmondia c. cardinalis</i>						PM	SM	PM
Rose-breasted grosbeak <i>Hedymeles ludovicianus</i>							SM	SM

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prisiere)	Decodon-Typha Associates (Swamp prisiere)	<i>Juncus-Scirpus</i> Associates (Swamp subserie)	<i>Chamaedaphne calyculata</i> Consociates (Bog prisiere)	<i>Nemopanthus-Alnus</i> Associates (Bog prisiere)	<i>Cephalanthus-Alnus</i> Associates (Swamp prisiere)	<i>Larix-Acer-Betula</i> Associates (Bog prisiere)	<i>Acer-Ulmus-Fraxinus</i> Associates (Swamp prisiere)
Eastern goldfinch								
<i>Astragalinus t. tristis</i> ....						SP	SM	SM
Red-eyed towhee								
<i>Pipilo e. erythrophthalmus</i>					SM	SM	SM	SM
Slate-colored junco							SM	
<i>Junco h. hyemalis</i> .....								
Eastern tree sparrow								
<i>Spizella a. arborea</i> .....			SP winter			SP winter		
Swamp sparrow								
<i>Melospiza g. georgiana</i>		SP	SP	SM	SP	SP		
Appalachian song sparrow								
<i>Melospiza melodia</i>								
<i>euphonia</i> .....		PM	SM	SP	SP	SP	SP	SP
MAMMALS								
Virginia opossum								
<i>Didelphis v. virginiana</i>		SM	SM			PM		PM
Hairy-tailed mole								
<i>Parascalops breweri</i> .....					SM	SM		SM
Star-nosed mole								
<i>Condylura cristata</i> .....		SM	SM					PM
Canada shrew								
<i>Sorex c. cinereus</i> .....		PM	PP	PM	PP	PP	PP	PP
Smoky shrew								
<i>Sorex f. fumeus</i> .....			SM			SM	PP	
Short-tailed shrew								
<i>Blarina b. brevicauda</i>			SP		PP	PP	PP	PP
Eastern raccoon								
<i>Procyon lotor lotor</i> .....		SM	SM			PM		PM
New York weasel, <i>Mustela</i>								
<i>frenata noveboracensis</i>						PM	PM	PM
Common mink								
<i>Mustela vison mink</i> .....		PM	PM			PM		PM
Eastern red fox								
<i>Vulpes f. fulva</i> .....		SM	PM			PM		PM
Southern woodchuck								
<i>Marmota m. monax</i> .....								SM
Southern red squirrel								
<i>Sciurus hudsonicus loquax</i>							PP	PM
Small east. flying squirrel								
<i>Glaucomys v. volans</i> .....							PM	PM
Northern deer mouse								
<i>Peromyscus leucopus</i>								
<i>noveboracensis</i> .....		SM			PP	PP	PP	PP

TABLE 8 (Continued)—Ecological Classification of Northeastern Ohio Hydrarch Species.

Species	<i>Nymphaea advena</i> Consociates (Swamp or bog prisiere)	Decodon-Typha Associates (Swamp prisiere)	Juncus-Scirpus Associates (Swamp subserie)	<i>Chamaedaphne calyculata</i> Consociates (Bog prisiere)	Nemopanthus-Alnus Associates (Bog prisiere)	Cephalanthus-Alnus Associates (Swamp prisiere)	Larix-Acer-Betula Associates (Bog prisiere)	Acer-Ulmus-Fraxinus Associates (Swamp prisiere)
Gapper red-backed vole <i>Clethrionomys g. gapperi</i>							PM	
Eastern meadow vole <i>Microtus p. pennsylvanicus</i>		PM	PP		PP	PP	PP	PP
Common muskrat <i>Ondatra z. zibethica</i> .....		PP	PP			PM		
House mouse <i>Mus m. musculus</i> .....			SP			PM		PM
Hudson Bay jumping mouse <i>Zapus h. hudsonius</i> .....		SP	SP		SP	SM	SM	SM
Mearns cottontail <i>Sylvilagus floridanus</i> <i>mearnsi</i> .....		SM	PM		PM	PP	PM	PM

## General Discussion

Through the process of succession all of the bog and swamp communities now present in northeastern Ohio have developed by gradual, constantly changing stages from a body of open water resting upon a bed of freshly deposited glacial silt. In its simplest aspects this process, largely biotic, consisted of slow building up of the bottom by the deposition of remains of organisms, together with some marl and silt. As the margins of the pond moved inward upon the open water they were followed by available plants and animals in progressive order according to their tolerance of water and their ability to compete with one another for space and light. The gradation of species thus produced, resulted in the formation of well defined although intergrading zones of life; from the floating plankton and fish of the deep open water, through the floating vegetation and accompanying animal life of the shallow water, the sedge and peat moss mat extending out over the shallow water from the shore, the bog heaths and shrubs which invaded the mat when it became solid enough, the bog forest which succeeded the shrubs and finally the spruce-fir climax forest, which, it must be remembered, was the climax type soon after the retreat of the Great Glacier.

Coincident with succession as thus described succession caused by changes in climate was also taking place. As the climate became warmer and dryer with the recession of the glacier in Post-Pleistocene times, pine and hemlock replaced the spruce and fir as climax species. For some reason, possibly because of the more constant ground water supply, the seral communities of the

hydrarch succession were not influenced as much by the change in climate and the communities leading up to the climax pine-hemlock were not radically different from those in the succession to spruce-fir. As climatic succession continued and warmer conditions prevailed, causing the pine-hemlock climax community to give way to a deciduous forest, the hydrarch communities at last began to be radically altered from a bog to a swamp condition. Evidence of these changes are found in the stratified pollens found preserved in the peat of the bogs themselves by Sears (1932) and other investigators. Despite the changes wrought by climatic succession communities of the hydrosere in general have suffered less alteration than either those of upland seres or the climax community itself, resulting in the presence today of so-called "relic bogs." The reasons are possibly lower temperature and a more constant water supply in the deep glacier-produced pockets, favoring the boreal species, or some soil property such as hydrogen-ion concentration, lack of oxygen, or available nitrogen less tolerated by the southern invaders than by the boreal species, or more likely a combination of these factors that have given the northern forms more protection against replacement by southern types on peat deposits than on better drained areas.

Local variations in the present day climate resulting from topography very likely aid the survival of relic species in certain localities. Such markedly lower average annual temperature, shorter growing season, and higher annual precipitation, particularly in snowfall, as one finds on the Appalachian Plateau in northeastern Ohio, in comparison with the conditions on the Lake Plain of the region (see section on climate), could hardly fail to be more favorable to the persistence of boreal relics there, and this is found to be the case, particularly in the bog depressions where water and cold air drainage have intensified the more general climatic effects. Besides, as first suggested by Dachnowski (1912), the Lake Plain may have been first exposed to colonization by land plants and animals after the majority of the boreal species had retreated to the north of Lake Erie in the wake of the ice sheet.

Peat deposits that have accumulated in pockets formed by the glacier on the Appalachian Plateau tend to be highly acid (Table 1). High acidity is apparently an indicator of certain chemical qualities of the soil which react unfavorably on the physiological processes of most plants, probably chiefly through water absorption and nitrogen availability. Certain northern plants seem to be more tolerant of these unfavorable soil conditions possibly partly through transpiration control and partly through specially adapted roots for the harboring of nitrifying bacteria which are capable of producing available nitrogen under acid conditions. High concentration of hydrogen-ions which reaches its maximum in the early stages of the bog forest seems to have a very definite positive correlation with the success of the bog species in the competition with swamp forms, although it may not in itself be the most limiting factor. In fact it has been observed that when relic boreal communities are cut over the new growth coming in is of a more southern aspect, indicating that competition from already established species is also of considerable importance in checking climatic succession. However, according to Salter and McIlvane

(1917), Tarr and Noble (1922), and others, acidities around pH3 are very unfavorable to the growth of the few species they studied by means of the water culture method. This would seem to indicate that probably there are many species which would be unable to tolerate soils with a pH around 3, such as the writer has found in the best remaining representatives of the bog forest communities in northeastern Ohio. Thus relieved from the competition of many species that are unable to grow vigorously in soils with such acid reactions, the few "relic" northern forms, more tolerant of high acidity, persist. In this same region boreal plants have been driven out of practically all places where hydrogen-ion concentration of the soil will permit the invasion of other species better equipped for competition under the present climatic conditions. Of course it does not follow that these northern species, which we find persisting in our bogs, grow better in these extremely acid soils than they would under more neutral conditions. In fact Moore and Taylor (1921) on the Maine coast and Young (1934) in the Adirondack Mountains found these plants growing well in much less acid soil where the climate, being more rigorous, probably relieves them of severe competition from species less tolerant of the cold. Whatever the other factors may be the writer's observations, together with those of Wherry (1920), indicate that in the southern part of their range, at least, the presence of certain boreal plants is definitely correlated with acid soil.

The occurrence of such boreal animals as the red-backed vole, and Grinnell water-thrush, definitely coincides with the occurrence of aggregations of boreal plants. Their persistence may be due partly to the direct influence of certain of the factors, such as temperature or constant moisture mentioned as possibly favorable to the persistence of the relic plants, partly due to the dependence of the animals upon the plants themselves, and partly due to lack of competition from southern invaders of the same ecological niche. More exact measurements of environmental factors of typical boreal habitats in their normal geographic location are necessary before any comparisons can be made to determine possible points of likeness between conditions in the relic boreal communities and those of the north. Whatever the case may be there seems to be no factor in the relic boreal habitat that is prohibitive to such characteristically southern species as the cardinal and the tufted titmouse, that are found even in communities with the greatest concentrations of relic boreal plants. Southern species are apparently not as common in these communities, however, as in the corresponding ones of the swamp sere.

Although the more typically bog types of communities can be readily distinguished from the swamp types by the major differences in appearance created by the primary dominants, it is sometimes impossible to say which species are more characteristic of bogs and which of swamps. Climatic succession has progressed so far that it is now unsafe to say that there are any species of the swamp sere which are never found in the bog sere in northeastern Ohio. On the other hand there are certain bog species (listed in Table 8) which seem to be dependent upon a bog habitat and are not found in places where climatic succession has progressed to the point that the commun-

ity is more swamp-like than bog-like. These are: tamarack, purple chokeberry, alderleaf buckthorn, Labrador tea, leatherleaf, mountain holly, hobblebush, withe-rod, swamp dewberry, large cranberry, Virginia cotton-sedge, white beak-rush, round-leaf sundew, buckbean, pitcher-plant, goldthread, yellow clintonia, dwarf dogwood, yellow-bellied sapsucker, Wilson trush, Grinnell water-thrush, magnolia warbler, blackburnian warbler, Canada warbler, slate-colored junco, red-backed vole, and the smoky shrew.

In the interpretation of any community in a hydarch series it is very important to take into consideration whether the community is the result of primary or secondary succession. The latter may be the result of interference with the orderly progression of biotic succession by human or physiographic agencies. Secondary succession is initiated when part or all of the organisms of a community are destroyed without complete destruction of the substratum which has been built up as the result of biotic reaction. This destruction is commonly brought about by lumbering, burning, or flooding of an area. The type of community resulting from secondary succession may be similar to or radically different from those of the prairie depending upon the nature and extent of denudation of original organisms and interference with the substratum. Usually the substratum of the original community is not entirely destroyed and secondary succession begins with a more advanced stage than primary succession (i.e., marsh instead of open water). Also as mentioned above secondary succession is more apt to conform in species composition to the present climatic conditions. In other words, when boreal relic communities are artificially removed from a northeastern Ohio area they are usually replaced by communities of more southern species. Jackson (1914, p. 48) also found this to be true in cut over areas of a bog in Wisconsin. Thus by greatly reducing the factor of biotic competition, considered so important by Clements, Weaver, and Hanson (1929) climatic succession is greatly accelerated. Although the communities of the subseries may be considerably different from those of the prairie the ultimate stage theoretically is the same—the present climatic climax type.

Generally speaking, in progressing from the early to the later stages of hydrarch succession the change in plants is from life forms of a hydric type to a more mesic type and in animals from aquatic to terrestrial. The transition takes place gradually but is most noticeable in the emerging stage where semi-aquatic plants occur and where typical amphibian vertebrates, the frogs, reach the peak of abundance. The reason for succession of animals is unquestionably dependent upon such complex combinations of factors that very little can be said on the subject without considerably more physiological experimentation upon the various species concerned than has already been carried out. Only the more obvious factors can be pointed out here. It is, for example, obvious that the change from the aquatic life form represented by the various fish through the amphibious life form represented by the frogs, to the terrestrial life form represented by mice is controlled primarily by the decrease in the amount of water in the environment. This in turn is controlled primarily by the deposition of organic matter and silt brought about chiefly by plants.

The next most obvious factor in the distribution of animals is the life form of plants which in turn is in part dependent upon the water content of the substratum. The pied-billed grebe, which is adapted to obtaining all of its food from the water, and requires only the minimum amount of vegetation to support its floating nest, is the first bird to appear in the hydrarch succession and is the least dependent directly upon vegetation of all of the warm-blooded animals with which we are here concerned. The red-winged blackbird, rails, and prairie marsh wren, are much more dependent upon vegetation for their food and the support of their nests, but the slender grass-like vegetation of the emerging stage is sufficient for their purposes, although not affording much protection against climatic conditions. The shrub stage, which succeeds the marsh, presents a plant life form which offers more secure support for nests and greater protection against climatic forces, such as wind and sunshine, and so attracts such animal life as the yellow warbler, alder flycatcher, and deer mouse. It seems to be the life form of the dominant plants and not directly the water conditions of the habitat that is important in bringing in these species, since they nest in priseral shrub communities with a much wetter substratum than that of a secondary succession marsh community near by, where, of course, they do not occur because of lack of proper support for their nests. The disappearance of the yellow warbler and alder flycatcher as shrub is succeeded by forest may be linked with decrease in light intensity since this is the most conspicuous change in going from one stage to the other. There is no lack of favorable nesting sites. The shrub stratum of the forest would still supply support for nests. The light factor is, of course, dependent upon the life form of the dominant plants.

We see then that in a general way succession of animals is correlated with plant life form, but there is a much greater range of habitat selection in the case of most animals than in plants; probably due in part to the greater mobility of the former. For instance, the deer mouse is the most consistently abundant species of vertebrate animal in both the forest and shrub stages and is even found breeding in the cat-tail community. The wood frog and spring peeper also range through the marsh, swamp shrub, and swamp forest commonly throughout the course of the year. In the case of these wide ranging species of animals there usually is a distinct seasonal change in the animal's habits, such as the completely different stages in the life form of amphibians. In any case there must be an adaptation to meet the change in environment. The deer mouse may rear its young in a confiscated marsh wren's nest in the marsh, a deserted alder flycatcher's nest in the shrub zone and a hollow birch stub in the forest community. Red-winged blackbirds were found to build their nests in buttonbushes after the shrub community had succeeded the *Juncus-Scirpus* marsh in which they had formerly suspended their nests in the slender rushes.

Elton (1927, pp. 11-12) has suggested the classification of animals as "exclusive" to a community if they are definitely confined to it, and "characteristic" of a community if they occur there in large numbers although not necessarily confined to it. Among the animals listed in Table 8 all are characteristic of one or more communities in which they are listed as predominants,



but none are exclusive to any one community. For all practical purposes it is probably better not to consider any vertebrate animal exclusive to any community of the hydrosere in northeastern Ohio, but rather as more or less characteristic of it.

Comparing the average number of pairs of breeding birds in the various associates (Table 6), it is found that the greatest population density is in the shrub communities, the lowest in the forest, while the marsh communities are intermediate with respect to population density. In the case of the small mammal populations (Table 7) the greatest density was found in the shrub zone, also; the lowest in the marsh, while the forest communities were intermediate. It seems obvious that the shrub communities are better suited than any others to support a larger population of both birds and mammals. The reason is very likely that in many respects the shrub zone is an intermediate stage between marsh and forest, combining some of the elements of each with some distinctly its own. The shrub communities offer very favorable nesting sites for birds from the standpoint of both support and concealment. Some of the species of birds like the red-winged blackbird, which nest in this zone, feed primarily in the marsh while others like the catbird go to the forest to seek food. Thus the total population has a great variety of possibilities for feeding. The same is also probably true of the small mammals.

A fact which does not show in Table 6 of average populations is the great annual fluctuation of abundance of breeding birds that occurs in the same hydrarch community. For example in 10.5 acres of Common rush-Woolgrass Associates the population of red-winged blackbirds fluctuated as follows from 1932 to 1939 (no census being made in 1935): 9, 15, 7, 0, 7, 23, 22 pairs. This amazing fluctuation coincided with the water content of the substratum that was in part dependent upon the spring and summer rainfall and in part a result of artificial tampering with the water level of the adjoining pond. It is significant that the red-winged blackbird population in a wetter 4.1 acre area nearby, supporting Buttonbush-Smooth Alder Associates, except for one year (1938) varied in the opposite direction from the marsh population as follows: 8, 2, 5, 12, 4, 8, 3. This indicates a change of nest sites from marsh to shrub in the dry years. A less pronounced fluctuation, also coinciding with the water level of the marsh, occurred in the prairie marsh wren and swamp sparrow populations. In a 23-acre area of Red Maple-Yellow Birch Associates the yellow-throat and song sparrow populations fluctuated violently during the six years from 1933 to 1939 (excluding 1935) as follows: yellowthroat pairs—4, 0, 4, 0, 5, 5; song sparrow pairs—1, 2, 1, 0, 3, 9. The populations of both of these species coincided in general with the abundance of sedges and grasses in the ground cover which in turn varied directly with the water table of the substratum.

In the larger geographical sense it seems that the distribution of plant and animal species in the hydroseres of eastern North America must be controlled primarily by climate, but within any given hydrosere of northeastern Ohio it is controlled primarily by water content of the habitat. The life form of the dominant vegetation, in turn controlled by climate and water content of sub-

stratum dictates the specific composition of subdominants and most animal life. The species of the dominant plant is of comparatively little importance to vertebrate animal distribution judging by the fact that relatively few species of boreal animals have persisted in even the communities of greatest concentration of relic boreal plants. In such communities the animals are predominantly southern in species composition, although there is some indication that these species are not in the same numerical strength as they are in the corresponding swamp communities. The few relic boreal animals mentioned above, which have persisted in the bogs of northeastern Ohio, very likely owe their presence there not only to the existence of suitable habitat but more important still to the retardation of competition from southern species of the same ecological niche which, up to the present time, for some reason have failed to become abundant.

From the foregoing discussion it seems that the present day composition of any hydrarch community in northeastern Ohio is the result of many interacting factors, some obvious, some obscure, and some probably not even yet thought of. Outside of the most important factors of climate and water content of substratum it seems unwise to attempt a relative evaluation of the various factors because of their close interrelationship, their dependence on one another, and the fact that probably they effect no two species exactly alike. Pending much greater advancement in our knowledge of the effect of specific factors on specific organisms the best we can do is to acknowledge that the sum total of all environmental, genetic-evolutionary, and distributional factors, including the interaction of the organisms themselves, in any community is responsible for the specific and numerical status of its plant and animal composition. The dynamic ecological forces that, under the modifying influence of all the factors mentioned above, bring about both biotic and climatic succession, are invasion, competition, and elimination.

### Summary and Conclusions

1. Physiographic factors have combined to make northeastern Ohio particularly rich in small, undrained bodies of water essential to the formation of certain types of bogs and swamps. The Pleistocene glaciers scooped out hollows and dammed up old valleys and when these depressions occur on the water-shed divide between Lake Erie and Ohio River basins the postglacial drainage system has not yet developed to the point of completely draining them. Impervious heavy clay bottoms and water supply from sandstone springs tend to keep the water level of these hydrarch areas constant.

2. Northeastern Ohio encompasses portions of two of the major physiographic provinces of the United States, the Central Lowlands and the Appalachian Plateaus. Climatic conditions of these two physiographic segments differ considerably from one another, averaging in annual temperature 47.5° for the plateau, and 49.2° F. for the lowlands; in length of growing season, 135 and 202 days; in annual precipitation, 40.2 and 33.4 inches; and in annual snowfall, 63.3 and 29.7 inches.

3. Instrumental studies show that modification of air temperature is brought about by the vegetation of a community, particularly during the season of leafage, the greatest influence being exerted by forest and least by marsh, with greater control produced upon maximum than upon minimum temperatures.

4. Relative humidities are high in all hydrarch communities compared with more or less equivalent stages on the upland. This is reflected in rate of evaporation which is 2.6 times greater in an upland grassland than in a rush-woolgrass marsh; and in an upland beech-maple forest is 1.8 times greater near the ground than in a red maple-yellow birch bog forest.

5. Northeastern Ohio is completely within the limits of the mixed mesophytic association of the Eastern Deciduous Forest Biome of the Upper Austral Life Zone. Elements of the White Pine-Sugar maple-Hemlock Association of the Northern Conifer-Deciduous Forest Ecotone of the Transition Life Zone exist, however, as relics or fragments of a post climax, chiefly on the Appalachian Plateau.

6. This blending of life zone elements or biomes produces hydrosere of two types; the bog, in which the plant species and major aspects of communities are more characteristic of succession to a northern coniferous forest climax; and the swamp, characteristic of succession to a deciduous forest, which, being the type normal under the present climatic conditions, predominates in northeastern Ohio. Factors involved in the persistence of boreal relics in localized areas probably are lower temperature, constant water supply, and high acidity, combined with the advantage of previous establishment in competition against invaders.

7. Communities resulting from secondary succession may be similar to or radically different from those of the prisere, depending upon the nature and extent of denudation. Usually the subsere begins with a more advanced stage than the prisere, because of incomplete destruction of the original substratum, and is more apt to conform in species composition to the present climatic conditions; that is, the new community coming in after denudation, instead of being a submerged or floating stage may be of a sedge meadow or shrub type if the denudation is merely the cutting or flooding of a bog forest, and the plant and animal components are not relics but of a more southern type.

8. Although there are a few northern species of animals that are restricted to typically bog habitats there seems to be no factor there completely prohibitive to certain southern species, which, however, are in lesser concentrations than in the corresponding swamp stages.

9. The hydrarch communities of northeastern Ohio are classified according to their position in biotic succession and their relationship to the bog or swamp sere (Table 5), and named after their primary dominant species.

10. In typical northeastern Ohio hydrarch succession the change in life

form is from aquatic plants and animals through semi-aquatic plants and amphibious animals to mesic plants and terrestrial animals.

11. The greatest populations of breeding birds and small mammals are in the shrub communities. The *Juncus-Scirpus* associes supports the second largest population of birds and is third for mammals; the forest communities are third for birds and second for mammals.

12. Annual fluctuations in abundance of certain species are correlated with water level.

13. It is better not to consider any representative plant or animal as exclusive to any one community but rather as more or less characteristic of it.

14. In the larger geographic sense climate in conjunction with genetic-evolutionary factors and physiographic barriers control the specific composition of the plant and animal life of an area. This condition is modified locally such as in the hydrarch communities of northeastern Ohio, chiefly by the water content of the soil. Lesser factors are produced by the organisms themselves, chief of which is the life form (not specific composition) of the dominant species, which modifies other factors such as temperature and light intensity.

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## Some Plankton Relationships in a Small Unpolluted Stream

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### Introduction

Work dealing with protistan stream plankton has repeatedly posed the question: "What is a normal stream plankton?" The answer to this is of necessity a qualified answer, as it is a practical impossibility to find two streams that are alike. Nevertheless, for the purpose of evaluating the effects of industrial wastes, sewage, and various drainages on the biota of streams generally, it becomes worthwhile to know the biota of a stream which, for practical purposes, is not subject to pollution. For such knowledge it is useful to start with the smallest stream having an all year flow. But do small streams have a plankton content?

Eddy (1934) stated that a point 57 miles from the source of the Sangamon River "may be considered as representing the stage of stream succession at which plankton production first develops." Shelford and Eddy (1929) considered Sangamon River water non-productive of plankton until it was 20 days old. Hutchinson (1939), however, found a sizeable plankton in the Hocking River at points hardly fifteen miles from the source of the river, and considered that pollution rather than age of water was responsible for plankton development in this instance.

Creeks are generally regarded as small streams and many creek samples received at this laboratory have shown far higher qualitative and quantitative plankton contents than the above paper indicate. Such was the case in Tanners Creek (Lackey 1942) where the unpolluted section of the creek, about 19 miles below its source, showed an average per sample of 36.45 species of protista and Rotifera, and an average of 1687 individuals per ml., in 29 samples taken over a period of about 9 months in 1940.

Evidently some small streams can and do develop large plankton populations independently of any single factor as age of water, presence of strong pollution, distance from source, and the like. It is also questionable whether such a population might arise from wide portions of such streams which in effect become ponds or lakes drained by the stream. Zacharias (1898) expressed the belief that river and lake planktons were different. This view may be extended to small streams as compared with small lakes and ponds, which though close to each other, may show radical biotic differences. Furthermore, Chandler (1937, 1939) has shown that typical lake plankton decreases rapidly in streams draining lakes. Reif (1939) observed the same thing happening in Minnesota streams. A similar decrease has been observed frequently

in the canal draining the impounded White River to the Indianapolis water purification plant. Butcher (1940) considers that stream plankton arises from the stream bed.

These actual or implied questions lend an added urgency to the necessity for knowing what might be expected in a small, relatively unpolluted stream. Unquestionably there are small streams which, because of speed of current, pollution or other factors, have practically no plankton. Some samples from creeks of fairly large size examined both at this laboratory and in the field, have shown almost no plankton. But the size of the stream is not indicative of its plankton content. A New Jersey "pool," spoken of elsewhere (1938) was actually the source of a small stream. It received its water supply directly at its upper end, and always had a current sufficiently strong to clear the water in a few minutes if it became roiled in sampling. Although free of contamination, in a year's study 171 species of protozoa were found in it, and a single sampling showed as high as 66 species, often present in high numbers. It may be objected that a stream 18 inches deep can hardly have plankton, but many of the forms in this body of water have been commonly treated as plankton. Size, or volume of water, then are only parts of the ecologic picture showing what might be expected in a stream.

#### Four Mile Creek Survey

Since the above discussion indicates a lack of data and knowledge as to plankton conditions in a small stream, a long time survey of such a stream was planned. That stream should be free of polluting influences at its head waters, and for an appreciable distance lower down. It should have an all year flow. And it should be accessible. The term average is difficult to apply to a stream, but it should not have too steep a gradient, nor yet be too sluggish. If unusual environmental factors, such as long stretches of artificially dredged channel, or long stretches choked with emergent aquatic vegetation are present, an attempt should be made to evaluate them.

A survey of the streams within sampling distance of the laboratory failed to reveal any with a yearly flow which did not get some pollution. Finally, Four Mile Creek in northwest Butler and southwest Preble Counties of Ohio, was selected. One small branch of this creek lies in Indiana. The creek, over its longest stretch, is approximately 40 miles long, emptying into the Great Miami River. It rises in the glacial drift uplands at an elevation of about 1200 feet, and empties into the Great Miami River above Hamilton at an elevation of about 580 feet. This gives an average slope of 15 feet per mile; however, much of this is in the upper reaches. There are four towns within its basin of 320 square miles. Fairhaven, population 125, is directly on the stream and is unsewered. College Corner is close to one branch, and Dartrtown is also close to the main stream. Oxford, population 6700, is the largest town lying near the main stream. It is a well sewered community, the sewage being treated by Imhoff tanks, trickling filters and a humus tank, and the system is reasonably efficient. On several visits to the creek below the outfall of the



sewage treatment plant no gross pollution was observed, there were fish in the stream, no odor was apparent but a small amount of *Sphaerotilus* was attached to some of the debris. There is practically no industrial pollution anywhere in the creek basin, so it receives only agricultural drainage and human sewage, most of that treated. The principal agricultural drainage is from grain fields and pastures. Sheep, cattle and hogs are numerous in the basin, and there are several dairy barns, but no milk treatment plants.

The condition of the creek above and below Oxford may be judged from six samplings in 1939-40. The lowest dissolved oxygen in these was 5.8 p.p.m., representing 57.3 per cent saturation. This was above Oxford, in September, about extreme low water. The highest 5-day biochemical oxygen demand of the stream above Oxford was 5.3 p.p.m., but all the other figures were about 1.0 p.p.m., and probably represent the normal condition of this stream. Below Oxford there is a rise in B.O.D. to about 2.0 p.p.m. Coliform bacteria are normally low, 2 to 110 per ml. above, and higher, 9 to 1100 per ml, below Oxford. Hydrogen ion concentration varied from pH 7.6 to 8.1. These results indicate moderate pollution below the town of Oxford. It should be noted that they constitute but a brief picture of conditions.

Stream flow records are not available, but in the winter and rainy seasons there is a good flow, and a summer rain serves to flush the creek. Due to the steep gradient and sandy bottom the water soon clears. It should be emphasized that this creek flows over a rocky bed, and that the deeper pools are separated often every hundred feet or so by riffles, over which a thin sheet of water flows, being well exposed to the biological film covering the stones of the riffle, and having ample opportunity to become oxygenated. In summer the flow drops greatly, but did not stop during the time of this survey. At Fairhaven, near the headwaters, it is stated that the creek flows all year. At times a very heavy bloom of phytoplankton is evident in the water, and on one occasion a pool in a portion of the stream bed had an enormous population. A similar pool on another occasion showed 72 species on analysis. In view of the rapid flow and short age of the water, it is apparent that those two factors alone are not sufficient to prevent plankton production.

Four sampling stations were selected. These were approximately three miles and one mile above Oxford, one mile below the Oxford Sewage Disposal plant outfall, and four miles below the third station. These are designated Station I, II, III and IV respectively. Between December 15, 1939 and October 13, 1941, ninety-eight samples were analysed, but regular sampling started January 21, 1941, and continued until October 13 of that year. No samples were taken in June because of continued rains and high, turbid creek flows, and none were collected in August due to the absence of the sample collector. Rains interfered with an occasional sample. Exclusive of Rotifera, 265 species, genera or groups of bacteria, algae and protozoa were counted.

Table 1 enumerates the organisms found in the creek, and shows the number of times each species occurred above the outfall of the Oxford Sewage Disposal Plant and below this outfall, within three temperature ranges. The

table is so arranged, because it is thought that temperature and the Oxford sewage entrance might represent the greatest modifying factors for the creek. Rainfall is of enormous importance in this respect, but its effects are summed up by the statement that a heavy rain quickly reduces the total population from source to mouth, and recovery occurs when flows again become normal or low.

Table 1 could have been materially augmented by adding those species which were observed at times, but in numbers less than one per ml., or by taking bottom samples. It could also have been greatly increased by identifying all species of *Scenedesmus*, *Chlamydomonas* and ciliates which were counted. But as representing the suspended or plankton forms, within 20 or 25 miles of the origin of a fairly swift, unpolluted creek, the list is impressive enough as it stands.

Five of the species found, *Vampyrella* sp., *Bodopsis godboldi*, *Salpingoeca brunnea*, *Cerasterias irregulare* and *Phacus hispidula*, have not been found by us in any other stream sample, although only *Cerasterias irregulare* is rare. Two other species, *Platymonas elliptica* and *Desmatractum* sp., have been common in this stream, but have never been found abundantly elsewhere by us. Neither was common for more than a brief period, and they only serve to bring sharply to attention how little we know of the environmental factors that call some species into a sudden great flowering. Actually, the species list for this creek does not show any organism that could be called characteristic of the stream. A number of species were either persistent or appeared in large numbers; that is, taking into consideration certain tendencies to be seasonal, to appear in turbid water, etc. But when this list is examined, it comprises those species which have so far shown the most widespread distribution in running waters. This lack of certain species sharply characterizing Four Mile Creek is good evidence that the creek is largely an unmodified typical one, for extremes, i.e., streams polluted by some particular type of waste, generally have some certain species not usually found elsewhere.

Another indication of the creek's nature is the size of the species list. Forty-one random samples from the Miami River into which Four Mile Creek empties, have shown only 236 (Lackey, unpublished data) species, genera or groups of algae and protozoa. And yet this river is about 180 miles long with a drainage of 5385 square miles. It also has a more gradual drainage and dams behind which water can age. The Scioto River, about 220 miles long, and with a basin of 6510 square miles, showed 448 species (Lackey 1941) but this comprised a study of 1400 samples over a period of three years. Tanners Creek, a few miles southwest of Four Mile Creek, but in the same drainage basin, is a much smaller creek. A very similar study of Tanners Creek showed in 84 samples, 227 species (Lackey 1942) but in its unpolluted portion 186 species. A comparison with other streams shows 203 species in the Cumberland and Duck Rivers (Lackey 1942) in a less extensive survey; 291 species in the San Joaquin River of California (Allen 1920) in an extensive survey; and 266 species in the Illinois River (Kofoid 1908) in an extensive survey. Other

TABLE 1.—Plankton Fungi, Algae and Protozoa of Four Mile Creek and the number of times each appeared in 100 ml. samples above and below the outfall of the Oxford Sewage Disposal Plant during three temperature ranges.

	Dec. - March 0°C. - 8.5°C.		April - May 9°C. - 80°C.		July - October 28.5°C.-13°C.	
	Above out- fall	Below out- fall	Above out- fall	Below out- fall	Above out- fall	Below out- fall
Total Samples	22	21	13	13	16	14
Thallophyta						
Fungi						
<i>Beggiatoa alba</i> .....		1		1		
<i>Blastocaulis sphaerica</i> .....					5	7
<i>Sphaerotilus natans</i> .....	1	9		6		7
Algae						
Myxophyceae						
<i>Anabaena</i> sp. ....					2	1
<i>Chroococcus limneticus</i> .....	3	1	1		4	3
<i>Chroococcus turgidus</i> .....					1	1
<i>Coelosphaerium Naegelianum</i> * .....	7	5		3		
<i>Lyngbya</i> sp. ....		2		1		1
<i>Lyngbya contorta</i> .....					1	
<i>Merismopedia glauca</i> .....			1			1
<i>Merismopedia tenuissimus</i> .....				3	6	9
<i>Microcystis incerta</i> .....					2	1
<i>Oscillatoria</i> .....	3	3	1	4	8	6
<i>Phormidium</i> sp. ....				1	4	4
Bacillarieae						
<i>Attheya zachariasii</i> .....					2	1
<i>Cocconeis</i> sp. ....			4	10		1
<i>Cyclotella meneghiniana</i> .....	13	9	11	9	10	7
<i>Cymbella</i> sp. ....	9	5	10	1	5	3
<i>Diatoma hiemale</i> .....	4	3		5		
<i>Eunotia</i> sp. ....	1					
<i>Gomphonema olivaceum</i> .....	10	3	4	5	7	4
<i>Gyrosigma</i> sp. ....	9	2	2		3	2
<i>Melosira granulata</i> .....	2	1	3		7	3
<i>Melosira</i> sp. ....					2	1
<i>Meridion circulare</i> .....			1			
<i>Navicula</i> sp. ....	20	19	12	11	15	11
<i>Navicula</i> minute forms .....	4	2				
<i>Nitzschia acicularis</i> .....	19	16	11	11	13	9
<i>Nitzschia sigmoidea</i> .....	12	5	6	2		
<i>Pinnularia</i> sp. ....					1	
<i>Rhizosolenia eriensis</i> .....						1
<i>Surirella</i> sp. ....	5	3	2		2	1
<i>Synedra actinastroides</i> .....	1					
<i>Synedra</i> sp. ....	17	11	9	4	1	1
<i>Synedra ulna</i> .....	20	19	9	7	7	8
<i>Synedra ulna</i> , var. <i>angustissima</i> .....			3	2	1	
<i>Synedra ulna</i> , var. <i>biceps</i> .....	10	7	4		1	1
Euglenophyceae						
<i>Cryptoglena pigra</i> .....	1	1			2	

\* Provisional name.

TABLE 1.—(Continued)

	Dec. - March 5°C. - 8.5°C.		April - May 9°C. - 80°C.		July - October 28.5°C. - 13°C.	
	Above out- fall	Below out- fall	Above out- fall	Below out- fall	Above out- fall	Below out- fall
<i>Euglena acus</i> .....	1		2		14	11
<i>Euglena anabaena</i> .....					7	5
<i>Euglena agilis</i> .....	2	1	1		1	2
<i>Euglena deses</i> .....					5	5
<i>Euglena fusca</i> .....					1	1
<i>Euglena gracilis</i> .....	1		1		2	1
<i>Euglena oxyuris</i> .....			2		1	2
<i>Euglena pisciformis</i> .....		1	1	4	12	9
<i>Euglena polymorpha</i> .....			10	7	12	12
<i>Euglena sanguinea</i> .....						1
<i>Euglena scioltensis</i> .....			1	2	9	10
<i>Euglena spiroides</i> .....			1	3	2	2
<i>Euglena tripteris</i> .....					4	4
<i>Euglena viridis</i> .....	2	2	8	11	14	9
<i>Euglena species</i> .....		2	1	11	13	10
<i>Lepocinclis marsoni</i> .....					7	7
<i>Lepocinclis ovum</i> .....				1	6	6
<i>Lepocinclis texta</i> .....					4	2
<i>Phacus anacoleus</i> .....	1				4	1
<i>Phacus hispidula</i> .....					1	
<i>Phacus longicauda</i> .....	1		1		5	2
<i>Phacus orbicularis</i> .....					1	
<i>Phacus pleuronectes</i> .....				1	5	4
<i>Phacus pyrum</i> .....			2	1	12	11
<i>Phacus Stokesii</i> .....					3	3
<i>Phacus triquetus</i> .....					8	6
<i>Phacus species</i> .....					1	2
<i>Trachelomonas crebea</i> .....	2	1	8	6	15	12
<i>Trachelomonas cylindrica</i> .....					1	
<i>Trachelomonas euchlora</i> .....			6	5		
<i>Trachelomonas hispida</i> .....		1	1	1	3	1
<i>Trachelomonas rugulosa</i> .....				1		
<i>Trachelomonas urceolata</i> .....			9	4	16	12
<i>Trachelomonas volvocina</i> .....	2		11	9	3	6
<i>Anisonema ovale</i> .....	1			1	1	
<i>Astasia dangeardi</i> .....			1	2		
<i>Copromonas subtilis</i> .....	1	1				
<i>Distigma proteus</i> .....			1			
<i>Entosiphon sulcatus</i> .....						1
<i>Euglenopsis vorax</i> .....					2	1
<i>Melanema variable</i> .....	1	1		1	1	
<i>Notosolenus orbicularis</i> .....		2	1	1		
<i>Peranema trichophorum</i> .....		1	1		1	1
<b>Dinophyceae</b>						
<i>Dinoflagellata, unidentified</i> .....			2		4	7
<i>Gymnodinium</i> sp. ....					2	2
<i>Gymnodinium gracilis</i> * .....			3	1	2	2
<i>Gymnodinium palustre</i> .....	3	2				
<i>Glenodinium</i> sp. ....						2

TABLE 1.—(Continued)

	Dec. - March 0°C. - 8.5°C.		April - May 9°C. - 80°C.		July - October 28.5°C. - 13°C.	
	Above out- fall	Below out- fall	Above out- fall	Below out- fall	Above out- fall	Below out- fall
<b>Cryptophyceae</b>						
<i>Chilomonas paramecium</i> .....			1	1		
<i>Chroomonas</i> spp. ....	16	15	10	8	10	7
<i>Cryptomonas erosa</i> .....	12	7	13	13	15	12
<i>Cryptomonas ovata</i> .....				3		
<i>Cyathomonas truncata</i> .....	2		1	2	2	
<i>Nephroselmis olivacea</i> .....			2			
<i>Rhodomonas lacustris</i> .....	1		2	2	1	3
<b>Heterokontae</b>						
<i>Centritractus belonophorus</i> .....			2	1	4	3
<b>Chrysophyceae</b>						
<i>Chromulina globosa</i> .....		1	5	6	1	1
<i>Chromulina ovalis</i> .....	15	13	3	2		
<i>Chrysamoeba radians</i> .....		1				
<i>Chrysochromulina parva</i> .....	2	1	3	1		
<i>Chrysococcus aspera</i> .....			4	2	3	
<i>Chrysococcus cylindrica</i> .....			1			
<i>Chrysococcus hemisphaerica</i> .....			1	1		
<i>Chrysococcus major</i> .....	2	2	2	2		
<i>Chrysococcus ovalis</i> .....		1		1	5	2
<i>Chrysococcus punctiformis</i> .....			1			
<i>Chrysococcus rufescens</i> .....	13	10	13	11	12	8
<i>Chrysococcus spiralis</i> .....			1			
<i>Dinobryon</i> spp. ....			1	1	2	
<i>Hymenomonas roseola</i> .....	1			1		
<i>Lagynion scherffeli</i> .....			2	2		
<i>Mallomonas akrokomos</i> .....		1				1
<i>Mallomonas large species</i> .....	4	2	4	1	3	5
<i>Mallomonas small species</i> .....	2	1		1	4	2
<i>Ochromonas</i> sp. ....		1		1		
<i>Physomonas vestita</i> .....			1	1	2	1
<i>Synura uvella</i> .....	2	1		1		1
<i>Chrysophyceae</i> , unidentified .....	1					
<b>Chlorophyceae</b>						
<b>Volvocales</b>						
<i>Carteria</i> spp. ....	1	1				1
<i>Chlamydomonas</i> , large spp. ....	13	18	9	10	16	13
<i>Chlamydomonas</i> , small spp. ....	1	1	2	2	1	2
<i>Chlorogonium elongatum</i> .....			1		3	4
<i>Collodictyon triculatum</i> .....			1		8	7
<i>Dysmorphococcus fritschii</i> .....					3	5
<i>Gonium pectorale</i> .....					3	2
<i>Gonium sociale</i> .....	1				1	
<i>Heteromastix angulata</i> .....				1	11	10
<i>Lobomonas rostrata</i> .....					4	2
<i>Mesostigma viride</i> .....			1	1	1	
<i>Pandorina morum</i> .....		1			3	4
<i>Pedinopera pyriformis</i> * .....						1

TABLE 1.—(Continued)

	Dec. - March 0°C. - 8.5°C.		April - May 9°C. - 80°C.		July - October 28.5°C. - 13°C.	
	Above out- fall	Below out- fall	Above out- fall	Below out- fall	Above out- fall	Below out- fall
<i>Phacotus angustus</i> .....					2	1
<i>Phacotus lenticularis</i> .....			11	6	14	11
<i>Polytoma granulifera</i> .....						1
<i>Platymonas elliptica</i> .....	2	2	8	8		1
<i>Ptermonas angulosa</i> .....				1	3	3
<i>Ptermonas plana</i> * .....						3
<i>Scherffelia phacus</i> .....	1	1	3		1	1
<i>Spermatozopsis exultans</i> .....			2		1	1
<i>Sphaerellopsis fluviatile</i> .....					2	4
<i>Thoracomonas phacotoides</i> .....			5	2	15	12
<i>Thoracomonas</i> sp. ....			5	2	15	12
<i>Wislouchiella planctonica</i> .....				1	1	6
<i>Pyramidomonas</i> sp. ....				2		
Chlorophyceae, sensu stricto						
<i>Actinastrum hantschii</i> .....			9	9	7	10
<i>Ankistrodesmus falcatus</i> .....			4	10	11	11
<i>Ankistrodesmus falcatus</i> var. <i>mirabilis</i> .....	1		10	8	8	11
<i>Ankistrodesmus falcatus</i> , var. <i>tumidus</i> .....				4	1	
<i>Cerasterias irregularis</i> .....						1
<i>Chlorella vulgaris</i> .....					1	
<i>Closterium acicularis</i> .....					7	7
<i>Closterium</i> sp. ....	1				1	
<i>Coelastrum microporum</i> .....				2	5	7
<i>Cosmarium</i> sp. ....					6	4
<i>Crucigenia apiculata</i> .....			1		4	3
<i>Crucigenia tetrapedia</i> .....	2	1	6	3		1
<i>Desmatractum</i> sp. ....					2	3
<i>Dictyosphaerium ehrenbergii</i> .....			9	7	13	11
<i>Golenkinia paucispina</i> .....			1	3	1	
<i>Golenkinia radiata</i> .....	1			1		
<i>Kirchneriella lunaris</i> .....			3	1	7	3
<i>Kirchneriella obesa</i> .....			4	4	1	4
<i>Lagerheimia brevispina</i> * .....				1	4	3
<i>Lagerheimia chodati</i> .....			3	2	2	3
<i>Lagerheimia quadriseta</i> .....	1		4	1	2	
<i>Lagerheimia subsalsa</i> .....					2	1
<i>Micratinium pusillum</i> .....			6	5	4	5
<i>Mougeotia</i> sp. ....					1	2
<i>Oocystis</i> spp. ....			6	2	8	8
<i>Ourococcus bicaudatus</i> .....						1
<i>Pediastrum boryanum</i> .....						2
<i>Pediastrum duplex</i> .....	1		1		5	7
<i>Pediastrum simplex</i> .....			1			2
<i>Pediastrum tetras</i> .....			1		3	1
<i>Polyedriopsis spinulosa</i> .....				1	1	1
<i>Scenedesmus spicatus</i> .....			7	6	12	6
<i>Scenedesmus</i> spp. ....	2		10	11	15	11
<i>Schroederia setigera</i> .....			2		1	3
<i>Selenastrum gracile</i> .....			1		3	3
<i>Tetradron caudatum</i> .....			3	4	8	8

TABLE 1.—(Continued)

	Dec. - March 0°C. - 8.5°C.		April - May 9°C. - 80°C.		July - October 28.5°C. - 13°C.	
	Above out- fall	Below out- fall	Above out- fall	Below out- fall	Above out- fall	Below out- fall
<i>Tetraedron hastatum</i> .....			1	1	1	1
<i>Tetraedron minimum</i> .....						1
<i>Tetraedron muticum</i> .....					3	4
<i>Tetraedron regulare</i> .....					3	3
<i>Tetrallantos lagerheimii</i> .....			2	1	3	6
<i>Tetrastrum anomalum</i> .....			3	2	10	11
<i>Tetrastrum heteracanthum</i> .....					2	2
<i>Tetrastrum punctatum</i> .....				1	8	7
<i>Tetrastrum staurogeniforme</i> .....			1	1	2	4
<i>Treubaria crassispina</i> .....				2	1	4
<i>Trochischia papillosus</i> .....			2		4	2
<i>Trochischia reticulata</i> .....			4	4	5	4
<i>Westella botryoides</i> .....			6	8	2	4
<i>Westella linearis</i> .....					1	
Green algal cells .....	12	12	14	16	10	8
Protozoa						
Mastigophora						
<i>Anthophysa vegetans</i> .....		1	1	3		
<i>Bicoeca lacustris</i> .....					1	1
<i>Bodo agilis</i> * .....		1				
<i>Bodo caudatus</i> .....	1	2				
<i>Bodopsis godboldi</i> .....		3	1			
<i>Cercobodo</i> sp. ....		1				
<i>Codonosiga botrytis</i> .....			1	3		1
<i>Copromonas subtilis</i> .....			1	1		
<i>Desmarella moniliformis</i> .....			1	2	1	
<i>Dinomonas vorax</i> .....				2	1	1
<i>Monas</i> spp. ....					3	3
<i>Oicomonas socialis</i> .....		1				
<i>Oicomonas termo</i> .....	5	6	7	10	2	2
<i>Oicomonas</i> sp. ....				2	2	
<i>Pleuromonas jaculans</i> .....					1	
<i>Salpingoeca brunnea</i> .....				2		
<i>Sphrochaeta</i> sp. ....		3	1			
<i>Trepomonas agilis</i> .....		1				
Sarcodina						
<i>Actinophrys sol.</i> .....	2			1		
<i>Amoebulae</i> .....		1		1		
<i>Amoeba radiosa</i> .....			2			
<i>Amoeba vesperilio</i> .....		1				
<i>Amoeba</i> sp. ....	2	2		1		1
<i>Chlamydomorphys stercorea</i> .....		2				
<i>Gocevia</i> sp.* .....						1
<i>Gromia fluviatilis</i> .....	1	1				
<i>Hartmanella hyalina</i> .....	1	3				
<i>Nuclearia simplex</i> .....			1		1	4
<i>Raphidiophrys elegans</i> .....					2	1



TABLE I.—(Continued)

	Dec. - March 0°C. - 8.5°C.		April - May 9°C. - 80°C.		July - October 28.5°C. - 13°C.	
	Above out- fall	Below out- fall	Above out- fall	Below out- fall	Above out- fall	Below out- fall
<i>Raphidiophrys pallida</i> .....		1			1	3
<i>Rudolfia</i> sp.* .....				1		
<i>Vahlkampfia albida</i> .....		1	1			
<i>Vahlkampfia guttula</i> .....		1				1
<i>Vampyrella lateritia</i> .....	2	1				
<b>Infusoria</b>						
<i>Aspidisca costata</i> .....	1	2		1		2
<i>Carchesium</i> sp. ....	1					
<i>Chilodonella cucullulus</i> .....	3	1		1		1
<i>Chilodonella uncinatus</i> .....	3	2			1	1
<i>Chilodonella</i> sp. ....	1				1	
<i>Cinetochilum margaritaceum</i> .....	3	4	2	3	2	5
<i>Codonella cratera</i> .....					1	1
<i>Coleps hirtus</i> .....	1		1		2	
<i>Colpidium campylum</i> .....		1				
<i>Colpoda</i> sp. ....	1					
<i>Cyclidium glaucoma</i> .....	4	5	3	5	9	8
<i>Cyrtolophosis mucicola</i> .....		1				
<i>Didinium balbiani</i> .....		1	1		1	2
<i>Enchelys vermicularis</i> .....		1				
<i>Frontonia leucas</i> .....			1			
<i>Glaucoma pyriformis</i> .....				1		
<i>Glaucoma scintillans</i> .....	1					
<i>Halteria grandinella</i> .....			5	2		1
<i>Hemiophrys</i> sp. ....	2	1	1			
<i>Holosticha</i> sp. ....	1	1				
<i>Lacrymaria olor</i> .....			1			
<i>Lembus pusillus</i> .....	4	4		1	2	1
<i>Lionotus fasciola</i> .....	2	3			1	
<i>Mesodinium</i> sp. ....	1					
<i>Microthorax sulcatus</i> .....				1		
<i>Oxytricha</i> sp. ....	4	7	1	3		1
<i>Phascolodon vorticella</i> .....					3	3
<i>Pleuronema chrysalis</i> .....	1		1			
<i>Stentor polymorphus</i> .....	1					
<i>Strobilidium humile</i> .....			7	4	4	5
<i>Strombidium</i> sp. ....						1
<i>Tintinnidium fluvatile</i> .....					1	
<i>Trachelocerca</i> sp. ....		1				
<i>Trochilopsis opaca</i> .....	1	1	1	1		
<i>Uroleptus</i> sp. ....	1					
<i>Urotricha farcta</i> .....	3		10	5	5	7
<i>Vorticella microstoma</i> .....				1		
<i>Vorticella microstoma</i> .....	2	2		2		1
<i>Cilata</i> , ave. 30 u. diameter .....	3	7	3	4	1	
<i>Cilata</i> , ave. 100 u. diameter .....					1	
<i>Suctorina</i> , unidentified .....				1		

\* Provisional name.

comparisons will be made in the future with the Ohio, and with the Licking and other Kentucky rivers.

It thus appears that at least some small streams develop an extensive plankton within a few miles of their headwaters. This is a logical development; when surface water drains into, or ground water reaches the surface to form the stream it normally contains an excess of nutrient matter dissolved from the soil, and this, together with the sunlight ought to be sufficient for the development of green plankton.

It should also contain some of the algae and protozoa commonly found in the soil (Sandon 1932) as well as bacteria. The bacteria and some of the protista are immediate food for other forms, and thus there is at once the possibility for a population. It is generally thought that the protozoa and algae are cosmopolitan, except that some are prevalingly marine, others prefer acid waters, etc. This fact is well borne out by the extensive lists which from time to time appear in technical journals; lists from all corners of the world. This work is now beginning to show that for some species a particular environmental factor is necessary or at least favorable, as the presence of  $H_2S$  favoring species of the ciliate *Metopus* (Hempstead and John 1939). A stream, unless its whole watershed is of a particular type, as some coal mine creeks in West Virginia, should be a highly generalized habitat. It is rare to find a stream which is truly an extreme environment. Some of the highly acid coal mine creeks are such, but even in coal mining regions highly acid streams are apt to be exceptions rather than the rule. It is more common to find a small stretch of stream which is locally highly changed, as by a large discharge of raw sewage. Modifications of the stream flora and fauna occur at such points. Usually they are catastrophic modifications. However, frequent additions of ground water and tributary streams, together with biochemical action, constantly tend to return the stream water to an "average" condition. A stream such as Four Mile Creek, getting practically no industrial pollution, and but little domestic sewage, ought to be an "average" stream, with its greatest modifications due to soil characteristics of its watershed. The kinds of organisms in the creek should be nearly similar at all four stations, unless the treated Oxford sewage makes a difference; no outstanding difference was actually found, except that total numbers were somewhat larger below the sewage treatment plant. This too, is in accord with what would be expected of a well treated sewage.

Finally, the absence of unusual species in abundance provides what might be termed a basic list for unpolluted streams which are slightly alkaline. Some forms which have been met with in other situations either frequently or in abundance, did not appear in a year's study of this creek. Since we suspect that most such forms appear in response to some specific pollutant as milk waste, sulphuric acid, etc., or in response to some unrecognized but critical factor, their absence here actually strengthens the idea.

Two general ideas may be derived from Table 1. First, the effluent from the sewage disposal plant did not exert any pronounced visible effect on the microscopic life studied. Second, there is a gradual increase downstream, of numbers of individuals, but not of species. About 28 species found above the

sewage outfall were not found below it, while 33 species found below it were not found above. Whether this gradual increase in numbers, as we go downstream, is due to sewage is a debatable question; time, normal multiplication, etc. all make it an unanswerable one at present. If a great influence of sewage was present, some new species should appear in large numbers and some others should decrease greatly. Nothing of this sort happens. Furthermore, almost all species peculiar to I and II or to III and IV appear only once or twice.

The Chrysophyceae, Cryptophyceae and certain species of Euglenophyceae, heretofore used as indicator organisms, fail to give clear cut results in respect to this question. Fifteen times when a full set of four samples was examined, *Chrsococcus rufescens* was highest at one of the two upper stations ten times and at one of the two lower stations five times. When this species was abundant, it was invariably highest at the upstream stations. Since we believe it to be very sensitive to sewage, these results are to be expected. On the five occasions when it was highest at the downstream stations numbers were low, the highest being 32 per ml., and data dealing with low numbers per ml. are more subject to experimental errors.

### Frequency of Organism Occurrence

#### A. GENERAL

It is theoretically possible for a plankton species to appear in every plankton sample obtained at a station. This would be 100 per cent of possibility, but for most species a much lower per cent of possible occurrence is actually found, especially if samples are taken over a long period of time. *C. rufescens*, however, occurred in a high percentage of possibility:

	Upper stations	Lower stations
December-March .....	59.1	47.6
April-May .....	100.0	84.6
July-October .....	75.0	57.1

The decrease downstream might be due to sewage, but if so, it merely accentuates the sensitive characteristic of this organism, and fails to show marked pollution, for in most random samples very few organisms ever occur even 47 times out of a possible hundred. There were twenty-two species of Chrysophyceae found, and they were well scattered in occurrence. The only other marked tendency exhibited in the group was the cold weather preference of *Chromulina ovalis* and the vernal predominance of *C. globosa*, which accord with records of their occurrence elsewhere.

Certain Cryptophyceae have also been deemed sensitive to sewage. *Chroomonas* sp. and *Cryptomonas erosa* had high percentages of possible occurrence:

	Upper stations	Lower stations
<i>Chroomonas</i> sp.		
December-March .....	72.7	71.3
April-May .....	76.9	61.5
July-October .....	62.5	50.0
<i>Cryptomonas erosa</i>		
December-March .....	54.5	33.3
April-May .....	100.0	100.0
July-October .....	93.7	92.3

Any downstream decreases, however, are small. In actual numbers, *Cryptomonas erosa* was highest at the upstream stations seven times and at the downstream stations five times, out of twelve times when it occurred in all four samples. Several times, it was equally abundant. On two of the occasions when it was most abundant downstream, the ratio was very high; 3400 to 30, one of these times. Obviously no marked effect of the Oxford sewage is apparent.

There was a large flora of Euglenophyceae but no single species ever attained great numbers. Only a few of the colorless members were counted, but they are distinctly bottom dwellers, whereas the green species are strong swimmers, often positively phototactic. The green members showed a strong preference for the hot weather months, and this is the time when the stream flow tends to be lowest, so that any effect of the Oxford sewage should be most evident. The temperature range, December through March was 0°C. to 8.5°C. and the total occurrence of green Euglenophyceae at all four stations was 1.4 per cent of possibility. In April and May the temperature range was 9°C. to 20°C. and the percentage rose to 14.5 at the two upper stations and 13.2 at the two lower ones. From July to the end of October the temperature ranged from 28°C. to 13°C. and the percentages of occurrence were 34.6 and 32.4 respectively.

These figures cover all the green Euglenophyceae found. Some of these are commonly met with both in the literature and in actual experience; others are rare. We have never regarded *Cryptoglena pigra* as common in streams, although occasional small blooms are encountered. *Phacus hispidula* was mentioned above as having been recorded in Four Mile Creek, the first and only time we have seen it in a stream. *Phacus pyrum* on the other hand is common in streams. *Euglena sanguinea* is rare in streams except for occasional blooms, but *Euglena acus* is common. If *Phacus hispidula* is normally expected (which it obviously isn't) in every 100 ml. sample taken, its occurrence is zero per cent of possibility except for the upper stations, July through October, when it is 6 per cent. *Euglena acus* on the other hand shows an occurrence of 87.5 per cent for the same stations at this time. While it is theoretically possible for a species to occur in all samples, except when the limiting factors for that species are known to be operative for a given sample, a much smaller frequency is usual, and such data enable one to speak of an organism as rare or common. The above figures for Euglenophyceae, July through October, may not mean that occurrence is dependent on temperature, for along with high temperature there were longer daylight hours, greater clarity of water, probably greater concentration of sewage plant effluent and a variety of other factors. But they do show the tendency toward recurrence in a given situation, and frequently it is possible to rule out certain factors, one by one.

No species of Euglenophyceae greatly favored the two lower stations. Various species were highest at the downstream stations 24 times and at the upstream stations 14 times, when full sets of four samples were examined. *Euglena viridis* was highest downstream six times; upstream four times. And yet when most abundant, unidentified species (probably a mixture of *E. agilis*, *E. pisciformis*, *E. anabaena* and similar ones) were four times more abundant

upstream; 160 per ml. and 40 per ml. The percentage of possible occurrence of the common species is high, July-October:

Species	Upstream Stations	Downstream Stations
<i>Euglena acus</i> .....	87.5	78.6
<i>Euglena polymorpha</i> .....	75.0	85.7
<i>Euglena viridis</i> .....	87.5	64.3
<i>Phacus pyrum</i> .....	75.0	95.7
<i>Trachelomonas crebea</i> .....	93.7	85.7
<i>Trachelomonas urceolata</i> .....	100.0	85.7

But if these figures are compared with the actual numbers present at the various stations, no decided downstream increase is apparent. Altogether the behaviour of the Euglenophyceae indicates no decided modification of the stream by the treated Oxford sewage.

Some other points of interest are brought out by Table 1. It is noted that *Sphaerotilus*, the sewage fungus, occurred 22 times at the lower stations and only once at the upper. Almost all of these occurrences were at Station III, closest to the sewage disposal plant outfall. Actually, this is the best indication by any organism that the creek receives sewage. Another bacterium *Blastocaulis*, the stalked form, was found only in the hot months.

Blue green algae were few in number and about evenly distributed in time and space. Diatoms were abundant, but the forms typical of large streams, as *Melosira* and *Stephanodiscus*, were practically missing as were lacustrine genera like *Tabellaria* and *Fragilaria*. *Nitzschia sigmoidea* seemed to be a cold water form.

The Dinophyceae and the Heterokontae were poorly represented, the latter by a single species, *Centritractus belonophorus*.

The Chlorophyceae were abundant in the warmer months. This was especially true of the Volvocales, except that motile cells counted as *Chlamydomonas* showed a very high percentage of possible occurrence at all four stations during the entire year. Some of these may have been motile reproductive cells of other Algae. *Heteromastrix angulate*, *Phacotus lenticularis* and *Thoracomonas phacotoides* showed high percentages of occurrence also. *Wislouchiella planctonica* seemed to be most abundant at the lower stations.

Other Chlorophyceae, mostly the small unattached Chlorococcales, were very rare during the cold months, reaching only 0.5 per cent of possible occurrence for all species at all stations, whereas their occurrence, July through October, was 28.1 per cent at the downstream stations, with several genera reaching 78 per cent. No definite preference for the downstream stations was found. Not infrequently, a single station of the four would show disproportionately large numbers, resembling a bloom of some species, as *Actinastrum hantzschii*, whose distribution on July 28, 1940, was:

Station I .....	0 per ml.	Station III .....	20 per ml.
Station II .....	4 per ml.	Station IV .....	448 per ml.

Such blooms occurred as frequently at one station as at another, and are more apt to represent the passage of a population downstream than to be of significance for the particular station at which they chance to be noted.

Protozoa were fewer in number than algae, and well scattered in distribution, both in time and space. This has been consistent behaviour of protozoa in streams and probably is related to the fact that they commonly ingest solid food, usually bacteria, occasionally algae or other protozoa. They are, therefore, mostly bottom dwellers, especially the saprozoic ones.

Some few flagellate members are characteristic of the plankton, and of these *Desmarella moniliformis* and *Dinomonas vorax* were found in Four Mile Creek. Other flagellate protozoa were largely adventitious. This was even more true of amoeboid protozoa, which appear to be almost lacking in the plankton of streams, although a few are always found.

The list of ciliates is more impressive, 38 species or genera having been identified. This includes a number of species which are definitely planktonic in habit as *Codonella cratera*, *Cyclidium glaucoma*, *Halteria grandinella*, *Mesodinium* sp., *Didinium* (*Monodinium*) *balbiani*, *Phascolodon vorticella*, *Strobilidium humile*, *Strombidium* sp., *Tintinnidium fluviatile* and *Urotricha farcta*. Of course, most of the species are adventitious, but the planktonic forms *Cyclidium*, *Strobilidium* and *Urotricha* showed the highest percentage of occurrence:

Species	Time	Stations	Stations
<i>Cyclidium glaucoma</i> .....	December-March .....	18.1	23.8
	April-May .....	23.0	38.4
	July-October .....	56.2	57.1
<i>Strobilidium humile</i> .....	December-March .....	0.0	0.0
	April-May .....	53.8	30.8
	July-October .....	25.0	35.7
<i>Urotricha farcta</i> .....	December-March .....	13.6	0.0
	April-May .....	76.8	38.4
	July-October .....	31.2	50.0

It has been pointed out elsewhere (Lackey 1938) that *Cinetochilum* and *Cyclidium* are widespread in occurrence and *Cinetochilum* is one of the commonest non-plankton ciliates in Four Mile Creek, while *Cyclidium* occurred more frequently than any other ciliate. Yet its maximum percentage of occurrence was 57.1 at the two lower stations in July-October. The occurrence with less frequency, of the remaining ciliates, is an indication of their adventitious nature, i.e., they normally live in or on the bottom film, and are passively swept up by the current, when found in the plankton. No decided preference for upper or lower zones is shown by any ciliate species; about the only decided trend for which they give evidence is the preference of the planktonic species for the warmer months.

In general, the above shown flora and fauna are abundant, varied, and show a gradual increase downstream, but not a sharp increase at either Station III or Station IV. A large increase had been anticipated at one or both of these stations, due to the addition of phosphorus.

## B. NITROGEN-PHOSPHORUS RELATIONSHIPS

One of the reasons for assuming that the effluent of a sewage disposal plant is such a potent modifying factor in a stream is that it enriches the stream with phosphates, nitrates and nitrites (see Table 3) which are generally assumed to be the critical substances necessary for the development of both animal and plant plankton. Unfortunately, there is considerable lack of agreement as to methods of determination of phosphorus, as to amounts used, and as to amounts necessary. Gessner (1934, 1939) says phosphorus concentration is the limiting factor for micro-organisms in the majority of natural waters, and gives figures showing that many lakes (including ponds?) had none. He concluded that phosphorus contributed in the sewage of towns falls rapidly, partly due to nonbiological formation of tricalcium phosphate, which is insoluble. This occurs because of the loss of  $\text{CO}_2$ . Harvey (1940) showed that if  $\text{CO}_2$  and pH are maintained in laboratory sea water aquaria, dense growths of normal plankton will develop in the aquaria, which does not happen when such aquaria are allowed to stand, with consequent decrease of  $\text{CO}_2$  and increase of pH. This maintenance of  $\text{CO}_2$ , of course, means more available phosphorus. Harvey also showed that diatoms used nine to ten times more nitrogen than phosphate in the aquarium cycle. Yoshimura, however, in a two year study (Yoshimura 1932) of nitrogen and phosphorus in a Japanese pond, found no correlation between plankton fluctuations and soluble phosphate, although high total phosphorus corresponded with high total plankton. This is in accord with the findings of Juday and Birge (1931) that soluble phosphate remained undiminished in the surface waters of Wisconsin lakes, many of them high producers of plankton. Actually, there is a cycle in the use of a certain amount of phosphorus which never becomes bound as tricalcium phosphate. Renn (1937) has shown this, although only small amounts of phosphorus may be involved. Apparently very small amounts of the element are sufficient to maintain the cycle although Lea (1941) indicates the amounts may be greater than assumed, because of the regeneration of phosphorus.

Because high plankton production had previously been noted in sections of streams presumably low in phosphorus, the amount of it at each of the four stations in Four Mile Creek was determined over a period of three months. Table 2 shows the amounts found, and it is readily apparent that the treated Oxford sewage contributed large quantities which were quickly used up or disappeared. The similarity of all four stations in respect to phosphorus on February 10 is due to high water, when soil phosphorus (it is far more abundant in soils than in most natural waters) was present.

The incoming sewage increased from 2 to 344 times the amounts of phosphorus present at Stations I and II. The rapid decrease between Stations III and IV is not wholly due to the formation of tricalcium phosphate; part of it was used by living organisms, because in addition to the green plankton, and the sessile green algae and other plants of the stream bed, there was an abundant non-green fauna, producing  $\text{CO}_2$ . Hence, despite the removal of  $\text{CO}_2$  by the green plants, resulting in the formation of tricalcium phosphate,



TABLE 2.—Amounts of  $PO_4$  in p.p.m. in Four Mile Creek on thirteen sampling dates in 1940.

Date	Station I	Station II	Station III	Station IV
1940				
January 27	.06	.04	.12	.08
February 3	.02	.02	.50	.05
February 10	.72	.72	.80	.72
February 17	.03	.04	.09	.04
March 3	.03	.03	.14	.02
March 11	.01	.01	.11	.04
March 17	.007	.007	.19	.04
March 24	.02	.025	8.60	.02
March 31	.015	.015	.19	.12
April 7	.015	.025	.125	.065
April 14	.02	.03	.34	.11
April 21	.02	.025	.32	.13
April 28	.017	.018	.46	.08

there was also a tendency to maintain the  $CO_2$  content. There are large numbers of snails in the creek which in warm weather use some calcium for shell making, but none of the more common marl forming plants.

It has long been known that in rivers, the lower third is generally plankton poor. Since nitrogen and phosphorus are generally considered the critical elements for plankton existence, a survey of the Scioto River made on July 31-August 1, 1940, is of interest in this respect. Plankton per ml.,  $NO_2$ ,  $NO_3$ , and  $PO_4$  were determined, the three chemical components in parts per million. Twelve stations were examined, from Columbus to Lucasville. Table 3 gives the values of the chemicals.

TABLE 3.—Amounts of Certain Chemical Components in p.p.m. at 12 stations on the Scioto River, July 31-August 1, 1940.

Station	$NO_2$	$NO_3$	$PO_4$
Scioto, above junction in Columbus .....	.02	1.0	.01
Olentangy, above junction, in Columbus .....	.01	.6	.01
Shadeville .....	.12	.2	.75
Commercial Point .....	.30		.60
South Bloomfield .....	.50	1.0	.45
Red Bridge .....	.20		.35
Pennsylvania R. R. Bridge .....	.10	1.0	.25
Mound City, Chillicothe .....	.04		.02
Chillicothe .....	.04	.35	NONE
Higby .....	.02	.10	NONE
Piketon .....	.002	.05	NONE
Lucasville .....	.001	.05	NONE

The rise in  $PO_4$  at Shadeville is due to the entrance above this station of the treated Columbus sewage. The noticeable decrease in  $NO_3$  and  $PO_4$  is correlated with a sharp drop in plankton (not shown) at the last two stations. Plankton was abundant at Chillicothe and Higby, despite the absence of detectable  $PO_4$  at those stations.

Apparently, however, extremely small amounts of phosphorus suffice for plankton requirements. A series of determinations were made for the Licking

River of Kentucky, October 16-17, 1940. The East Fork had high  $\text{PO}_4$  values, but plankton was low; the South Fork likewise had high  $\text{PO}_4$  values, but plankton was very high. In this case  $\text{PO}_4$  was 1.50 p.p.m. or higher at every station on the North Fork and 1.27 p.p.m. or higher at every station on the South Fork. Stream flow was low, and clear; the seasonal temperature was high and high plankton counts were expected. Despite the high  $\text{PO}_4$  values plankton was much lower in the North Fork and it appears that above a small but undetermined  $\text{PO}_4$  value, this element ceases to be a limiting factor, at least in some cases.

Two series of laboratory experiments illustrate this point. In one series, daily determinations were made on  $\text{PO}_4$  and flora and fauna, as well as bacteria ( $37^\circ$  agar counts) in a volume of sewage continuously aerated. This was activated sludge to begin with, but no food was added in the first experiment. Although aeration was continuous, the colorless forms (there were no green plant cells) soon disappeared, only an occasional one being seen after 10 days.

In a second activated sludge experiment, bottle A had the phosphorus content as  $\text{PO}_4$  maintained at about 24 p.p.m., while Bottle B was given no phosphorus. In B the  $\text{PO}_4$  disappeared after three days. At that time, bottle B had about 14 million bacteria per ml., whereas A (containing  $\text{PO}_4$ ) had about 237 million. In eleven days, the bacteria had declined to 5,430,000 per ml. in A and 2,060,000 per ml. in B, and A had 15 species of protozoa of which 5 were ciliates, whereas B had only 4 species of protozoa, one species being a ciliate, *Euplores* sp. It seemed impossible to attain a barren condition in such bottles, but this was due to the maintenance of a closed cycle; some of the bacteria constantly utilize decomposing plankton and the phosphorus they thus acquire again functions as they become food for an occasional ciliate or the two persistent flagellates, *Pleromonas jaculans* and *Oicomonas termo*.

In a third experiment of this series (Table 4) using activated sludge, bottle A was given 30 p.p.m. of  $\text{PO}_4$  and 500 p.p.m. of glucose on April 8. Bottle B was the same initially, but no  $\text{PO}_4$  was added, whereas the phosphorus in A was maintained by daily dosage. Bottle A constantly maintained a high plankton population until its glucose was depleted; this took 14 days and thereafter its population dropped at once, almost to zero. Phosphorus addition was discontinued in it on April 22. Table 4 shows the numerical changes in this experiment.

Bottle B lost its detectable soluble phosphorus in 4 days. Nonetheless, it maintained a small population of protozoa for 37 days, with a steadily declining bacterial population. It is inferred that this was due to two factors: (a) there was a constant use of glucose by bacteria, which used small amounts of phosphorus over and over again, (b) these bacteria served as food for the small protozoan population. At the end of 37 days (May 15) bacteria were very low, as were protozoa; glucose had dropped to 36 p.p.m. At this point, 1.5 p.p.m. of  $\text{PO}_4$  were added and both bacteria and protozoa increased in numbers, the former to 5,800,000 per ml. on May 22. These were responsible

TABLE 4.—Population trends in two bottles, one containing practically no  $P0_4$ , the other 30 p.p.m. Aeration continuous. Temp. 20°C. Glucose: 500 p.p.m. initially. Seed: Equally divided portion of an old activated sludge culture. Bacteria per ml. of seed: 22,600,000.

Date	Bottle A — 30 p.p.m. $P0_4$					Bottle B — No. $P0_4$				
	Bacteria per ml. in thousands	Protozoa			Nos.	Bacteria per ml. in thousands	Protozoa			Nos.
		Genera	Ciliates Nos.	Other Genera			Genera	Ciliates Nos.	Other Genera	
April 8	23,000 <sup>(a)</sup>	8		15	6048	50 <sup>(a)</sup>	8		15	
27 hours	76,000	1	72	6		4650	1	72	5	3816
April 9	126,000					4700				
April 10	650,000	0	0	6	60480	2820	1	216	5	8928
51 hours	770,000					1890				
April 11	164,000	2	1568	7	828448	1330	2	96	5	7104
April 12	90,500	3	14112	8	106272	1080	3	216	3	12240
April 13	23,500	4	9648	5	132408	815	1	72	1	15120
April 15	22,400	4	8784	8	159632	1260	3	792	5	12240
April 16	8,150	5	9036	9	134046	900	2	504	3	41040
April 17	8,700	3	14688	11	101520	1290	3	864	4	16056
April 18	6,150	3	32384 <sup>(b)</sup>	10	109080	1720	3	432	4	11160
April 20	5,600	3	7128	8	73800	2460	1	504	6	10800
April 22 <sup>(c)</sup>	4,300	1	1008	6	44640	1940	1	1512	4	9360
April 27		1	144	2	2880	975	2	2304	4	7200
May 15 <sup>(d)</sup>		1	72	2	2880	31	1	144	3	2160
May 16 <sup>(e)</sup>						3270	1	180	4	22536
May 20						5800	0	0	6	42624
May 22						520	5	2880	6	99840
May 24						2180	1	1200	4	8640
May 26						500	1	72	2	10800

(a) Viable bacteria 1.5 hours after seeding.

(b) Most of the ciliates looked starved.

(c) Glucose depleted.

(d) 1.5 p.p.m.  $P0_4$  added to B.

(e) Glucose 36 p.p.m. in B.

for an increase to 11 genera of active protozoa, of which 5 were ciliates but by May 26 both  $\text{PO}_4$  and glucose were no longer detectable, bacteria were again very low and the only protozoa were a few *Monas*, a few *Hartmanella* and an occasional ciliate, these latter being small and starved in appearance.

Two significant facts are shown by this last experiment. First, as long as ample phosphorus was present the attack on the food (glucose) present was vigorous. The use of phosphorus and of glucose seemed to be a function of the bacteria, which themselves maintained a fairly large bacterium eating protozoan population. Once the glucose was depleted, however, both populations immediately dropped to a minimum.

Second, in the absence of constantly added phosphorus but the presence of abundant food (glucose) there was a strong tendency to maintain a population cycle, utilizing traces of phosphorus possibly over and over. This population was much smaller, but fairly constant. It is also notable that the addition of phosphorus quickly stimulated either directly or indirectly the excystment of numerous protozoa.

The final experiment was an attempt to show whether laboratory maintenance of phosphorus and nitrogen would maintain a normal stream plankton. Four aquaria (A, B, C and D) of 10 or 12 liters capacity were filled with creek water, and illuminated by a fluorescent lamp for 12 hours per day. It had already been demonstrated that this source of light was ample for certain Chlorophyceae. There were no significant changes in pH, D.O. or temperature (once it was raised gradually from  $1^\circ\text{C}.$  to  $20^\circ\text{C}.$ ) in the aquaria and it is believed the osmotic character of the water was practically unaffected.

Initial populations were counted. While small, there were altogether 20 genera or species of which 18 contained chlorophyll. There were smaller, uncounted numbers of other species as well.

The mixed creek waters contained, in p.p.m.,

$\text{NO}_2\text{-N}$ .....	0.036	$\text{NH}_3\text{-N}$ .....	0.17
$\text{NO}_3\text{-N}$ .....	0.56	$\text{PO}_4$ .....	0.045

All aquaria were equally lighted, and constantly kept at a uniform water level by frequently adding small amounts of distilled water. Aquarium A was given  $\text{KNO}_3$  and  $\text{Na}_2\text{H PO}_4$  once weekly to maintain nitrogen and phosphorus. B was dosed weekly with  $\text{Na}_2\text{H PO}_4$ ; C was daily given a dose of 50 ml. of raw sewage, which gave it a dilution factor of 1 to 240, easily sufficient to prevent pollution. D was a control—nothing added. All were continuously aerated slightly. Weekly determinations of  $\text{PO}_4$ ,  $\text{NO}_2\text{-N}$ ,  $\text{NO}_3\text{-N}$ ,  $\text{NH}_3\text{-N}$  and plankton were made.

As far as the original intent was concerned, the experiment was a failure. Phosphates and nitrates increased in all but the control tank, and the normal stream plankton steadily dwindled and finally there were no green forms except

occasional *Scenedesmus*, and *Ankistrodesmus*, with a few round green cells, possibly *Pleurococcus*. Ciliates and colorless Euglenidae increased for a while, then gradually became few in numbers, except in the tanks getting sewage, which developed a large fauna, one resembling a sewage plant fauna. It thus appears that the maintenance of available nitrogen and phosphorus under laboratory conditions is still not sufficient for the maintenance or increase of a natural plankton population, at least of fresh water forms.

Experiments and stream analyses such as the above indicate that we are still far from understanding the nitrogen-phosphorus plankton relationships in streams or natural waters. They do indicate that extremely small amounts of these two elements in available forms are sufficient for large populations, and that an excess is not used, at least at the point where it is found in excessive quantities. It is also indicated that sewage plant effluents either exert more of an influence on bottom conditions than on plankton, or that their effects are long drawn out, influencing plankton conditions over many miles.

### Summary and Conclusions

1. A small, continuously flowing creek, largely subject only to agricultural and rural drainage was sampled at four stations for almost a year and its plankton content identified and counted.

2. A study of certain physico-chemical features was carried out and leads to the belief that the stream in question is largely an unmodified stream with an abundance of mineral salts, abundance of dissolved oxygen, low biochemical oxygen demand and with no extremes of environment.

3. The greatest potential modifying factor is believed to be the entrance of treated sewage. This is shown to greatly increase the  $\text{PO}_4$  content.

4. No great increase in plankton followed the increase in  $\text{PO}_4$  content, and by comparison with other studies it appears that a very low  $\text{PO}_4$  content is sufficient for a large plankton population, and that an excess exerts little or no influence.

5. A relatively large plankton population was present within a few miles of the headwaters, in water which was not aged to any great extent.

6. The plankton population of this creek is believed to represent a "basic" population, i.e., what might be expected in a small, slightly alkaline stream, relatively clear, slow flowing in some stretches, well oxygenated, of low B.O.D. and not subject to extreme pollution of any sort.

7. Comparative stream studies and laboratory experiments were made, attempting to evaluate the nitrogen-phosphorus plankton relationships due to the admission of large amounts of treated sewage.

8. Evidence of a definite biological cycle for the use of phosphorus was noted.

9. Extremely small amounts of phosphorus, possibly in excess of the amount often added by sewage, appear to be sufficient for abundant plankton production.

10. Apparently the excess of phosphorus is either removed non-biologically as insoluble tricalcium phosphate, or is used in the bottom film, which was not investigated.

11. As long as phosphorus is present in ample quantities, there is a rapid use of other food, at least organic food, but diminishing phosphorus below the critical point greatly retards the use of organic food.

12. Maintenance of excess available nitrogen and phosphorus in the presence of adequate light,  $O_2$ , small variations in pH, osmotic character, and temperature, still failed to maintain or provide a "normal stream plankton" in the laboratory.

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# The Photosynthetic Activities of the Aquatic Plants of Little John Lake, Vilas County, Wisconsin\*

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## Introduction

The fundamental organic matter produced by a lake is manufactured by the aquatic chlorophyll-bearing organisms from carbon dioxide, water and various other substances dissolved in the water and the manufacturing process is energized by the subsurface solar radiation. It represents the primary anabolic activity on which all aquatic life depends, either directly or indirectly, for its sustenance. Both the large aquatic plants and the microscopic forms of the phytoplankton contribute to the production of this organic material; generally speaking however, the phytoplankton plays a more important rôle in the manufacturing process than the large aquatics, especially in lakes that are deep enough to become thermally stratified in summer. The latter are usually confined to the shallow water where light and soil conditions are more favorable for their growth. The phytoplankton, on the other hand, is free floating and is distributed throughout the epilimnion due to the wind circulation of that stratum; it is present even in the lower water where conditions are not so favorable for photosynthesis.

In Little John Lake for example, the average standing crop of centrifuge plankton, consisting chiefly of phytoplankton, in the 0-4 m. layer at the time of these observations amounted to about 4200 kg. of dry organic matter as compared with some 90 kg. of dry organic matter in the large aquatics as previously reported by Wilson (1935); this gives a ratio of about 45:1. The transparency of the water is such that the large aquatics do not extend below a depth of 3 m. which includes only one-third of the area of the lake. While the phytoplankton organisms are small in size, they make up for this handicap by their abundance, wider distribution in the lake, and their rapid rate of reproduction, especially under favorable growing conditions in summer. Thus the annual production of organic matter by the microscopic forms will be much greater than that of the large aquatics because the 90 kg. of dry organic matter in the latter represented substantially the total crop for the year. The 4200 kg. of dry organic matter in the centrifuge plankton consisted of three constituents: (1) the phytoplankton, (2) the zooplankton, and (3) dead particulate material derived chiefly from these two groups of organisms, which is being

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broken up in the process of decomposition. The relative proportions of these three elements have not been determined for the centrifuge plankton of Little John Lake. At the time of these observations, the large aquatics had reached an advanced stage of maturity and were not very active from a photosynthetic standpoint, so that the changes noted in the dissolved oxygen content of the water may be attributed to the activities of the phytoplankton, especially in late August when the continuous record of the oxygen was obtained.

### Methods

A continuous record of the oxygen content of the upper water of Little John Lake was secured by means of four dropping mercury electrodes anchored at different depths, namely 0.8, 2, 3, and 4 m. The type of electrodes used in these experiments has been described by Manning (1940). The electrode at 0.8 m. was not operated any nearer the surface because waves interfered with its recording on windy days. The electrodes were suspended from a buoy located some 200 m. off shore where the water was a little more than 5 m. deep; they were connected to a Cambridge recorder on shore by flexible water-proof, three-wire cables. Four electrical thermometers were also installed on the buoy at the same depths as the electrodes; they too were connected to a continuous acting multithermograph recorder on shore by means of wire cables. The temperature readings were required for corrections that had to be made to the electrode records. Four rubber tubes were also installed on the buoy, one at each depth, with its intake opening near an electrode, so that samples of water could be pumped up from time to time without disturbing the electrode, for check determinations of the dissolved oxygen by the regular Winkler method.

Two difficulties encountered in the operation of the dropping mercury electrodes may be mentioned in this connection. It was found that they do not operate properly in very soft waters; that is, in those where the combined Ca and Mg content is less than 3 mg/l. In the harder waters the chief difficulty was due to the clogging of the capillary tubes through which the drops of mercury were discharged. To prevent this clogging the mercury had to be carefully washed in dilute nitric acid, filtered and kept scrupulously clean.

Both oxygen production and oxygen consumption were studied by the bottle method. For this purpose samples of water were taken from different levels of the 0.4 m. stratum and placed in glass stoppered bottles which were then suspended from the buoy at the same depths from which the samples were taken; they remained at the various depths for periods ranging from four hours to four days. Clear bottles in duplicate were used for the oxygen production and duplicate bottles covered with black paint were used for the determination of the oxygen consumed. The total quantity of oxygen produced is represented by the difference in the oxygen content of the water in the clear and in the black bottles. The oxygen content of the original water used for the samples was determined for a blank.

The plankton samples were obtained with a Foerst high-speed centrifuge

having a force equal to about 18,000 times gravity. Two sets of catches were taken with this instrument, one for numerical determinations of the phytoplankton constituents and the other for the gravimetric determination of the quantity of dry organic matter in the centrifuge material. Observation on the transparency of the water were taken with a Secchi disc and Dr. L. V. Whitney made readings of the penetration of solar radiation into the water with a pyrlimnometer in which the receiving element consisted of a Moll thermopile as described by Birge and Juday (1931). The chlorophyll determinations were made according to the method described by Manning and R. E. Juday (1941).

### Character of Lake

Little John Lake is situated in T. 41 N., R. 7 E., Sec. 20 and 29. It has an area of 67.2 ha. (166 a.), a maximum depth of 6 m. (20 ft.) and a mean depth of 3.77 m. (12 ft.). The total volume is 2,537,200 m<sup>3</sup> (3,318,650 cu. yd.) distributed as follows: 0-2 m. 1,196,200 m<sup>3</sup>; 2-4 m. 919,500 m<sup>3</sup>; 4-6 m. 421,500 m<sup>3</sup> (Juday and Birge 1941). The shores consist of the usual glacial material, such as sand, gravel and boulders of various sizes. Except in the region of two resorts, the upland surrounding the lake is covered with second growth timber. While the lake is comparatively shallow, the bottom slopes rather steeply from the margin of the water so that there is a large area in the center that is 5 m. or more in depth; in fact 39 per cent of the area of the lake lies inside the 5 m. contour line. There is a small outlet, but the outflow of water usually ceases sometime in late summer, especially in dry seasons.

The transparency of the water as measured with a Secchi disc ranged from 1.8 to 3 m., depending on the abundance of the plankton. The water has a low color, with readings ranging from 14 to 20 on the platinum-cobalt scale. The light penetration readings taken with the pyrlimnometer on August 22, 1941, showed that only about 10 per cent of the solar energy delivered to the surface reached a depth of 1 m. and only 4.2 percent went to 1.5 m. The amount was reduced to less than one per cent at 2.5 m. The conductivity or specific conductance of the water varies from 70 to 75 reciprocal megohms. Little John Lake was selected for these experiments because its water contains enough electrolytes for the successful operation of the dropping mercury electrodes and also because it usually has a fairly large standing crop of phytoplankton during the summer, which would insure daily oxygen changes large enough to be measured by the electrodes as well as by the Winkler method of oxygen determination.

### Temperature

While Little John Lake has a maximum depth of only 6 m., there is a definite thermal stratification of the water in summer as shown by the temperature results given in Table 1; a few additional temperatures are given in Table 4. During the greater part of the summer, the temperature readings are appreciably lower at 4 m. and below than in the upper 3 m. On August 2 for example, the temperature at 0.8 m. was 27.5° C., while that at 4 m. was 18.5°

a difference of 9°; the surface temperature was not taken in this series but it was probably somewhat higher than that at 0.8 m. Bottom temperatures as low as 17.5° have been noted at 6 m. in mid-July in previous years. The data given in Table 1 show that there was a gradual decline in the temperature of the water of the 0-3 m. stratum during the first half of August and after August 13 the maximum difference in the upper 4 m. did not exceed 2°. The results for oxygen also serve to bring out the stratification of the water during the first half of August.

### Mineral Content of Water

The mineral content of the water of Little John Lake is given in Table 2. The data show that the lake belongs to the group designated as medium hard waters. The various substances held in solution are present in sufficient amounts to satisfy the needs of moderate crops of aquatic plants and the plankton results given in Table 4 indicate this fact. The average bound carbon dioxide content of the water was 18 mg/l which was equivalent to a methyl orange alkalinity of 41 mg/l when expressed in terms of  $\text{CaCO}_3$ . On July 30, 1941, the pH readings were as follows: 0 m. 9.4; 1 m. 9.4; 2 m. 9.5; 3 m. 8.3; 4 m. 7.4. The high alkalinity in the upper 2 m. of water is due to the photosynthetic activities of the phytoplankton in that stratum. The average quantity of dry residue obtained from several samples of evaporated water was 57 mg/l as indicated in the table. The other items listed in Table 2 need no special comment. The quantity of the so-called "dissolved organic matter" varied from a minimum of 5 mg/l to a maximum of 13 mg/l and the oxygen consumed ranged from 3.6 to 6.2 mg/l.

### Dissolved Oxygen

The thermal stratification prevented the general circulation of the water at 4 m. until the latter part of August, hence the electrode placed at this depth gave near zero readings during the first half of the month. Owing to the low transparency of the water, very little photosynthesis took place at 4 m. during July and early August and the considerable quantity of organic matter coming chiefly from the plankton that settled into the 4-6 m. stratum consumed substantially all of the dissolved oxygen in this region during that time. For this period the quantity of oxygen at 4 m. ranged from a minimum of 0.1 mg/l to a maximum of 1.1 mg/l between July 30 and August 12, with a mean of 0.4 mg/l. Due to the cooling of the upper stratum with the advance of the season, the water at 4 m. began to take part in the circulation of the epilimnion on August 13 and the amount of oxygen found at this depth thereafter varied from 4 to 6 mg/l until complete circulation at that depth was fully established about August 20.

Table 1 shows that the 0-3 m. stratum of water had a fairly large excess of dissolved oxygen in early August; the same was true also of late July. A maximum of 15.0 mg/l was noted at 3 m. in the afternoon of August 5; this was equivalent to 167 per cent of saturation. A similar supersaturation was

TABLE 1.—Some temperature and oxygen observations made on Little John Lake during the month of August, 1941.

Date	Hour	Depth, meters	Temp. °C	Oxygen	
				Mg/l	Per cent sat.
Aug. 2	3:30 p.m.	0.8	27.5	9.3	112.3
		2	25.2	11.2	130.3
		3	21.0	11.3	122.4
	3:15	4	18.5	0.4	4.1
Aug. 5	3:45 p.m.	0.8	27.0	8.8	105.4
		2	23.7	9.4	106.8
		3	22.5	15.0	167.0
	4:00	4	19.0	0.1	1.0
Aug. 9	3:45 p.m.	0.8	26.2	8.8	104.1
		2	25.5	9.6	112.3
		3	25.0	10.4	120.6
	3:30	4	20.8	1.4	1.5
Aug. 11	3:45 p.m.	0.8	23.7	8.4	95.4
		2	23.5	7.8	88.3
		3	22.7	7.6	84.9
	3:55	4	21.5	0.8	8.7
Aug. 22	8:40 a.m.	0.8	20.0	6.4	68.1
		2	20.0	6.4	68.1
		3	19.8	6.1	64.7
	8:30	4	19.8	5.9	62.6

found at this depth on the previous afternoon (August 4), with a concentration of 14.6 mg/l which was equivalent to 162 per cent of saturation. After August 14 however, all of the determinations showed that the quantity of dissolved oxygen in the 0.4 m. stratum was well below the saturation point.

### Photosynthesis

The records obtained for oxygen with the four dropping mercury electrodes from midnight August 20 to midnight August 22, inclusive, are shown in Fig. 1. The four curves for the 24 hours of August 21 show the oxygen increases brought about by the photosynthetic activities of the phytoplankton during a day when the water was disturbed very little by wind, and when there was an alternation of clouds and sunshine, with a relatively small amount of cloud in the middle of the day. The four series of circles shown on the diagram for this day represent the results of the determinations made at the different depths by the Winkler method. It will be observed that the titration values check closely with those indicated by the dropping mercury electrodes. The maximum difference was noted at 4 m. at 2:30 p. m. where the titration result was 0.6 mg/l lower than that of the electrode. All of the other titration readings were much closer and most of them were identical by the two methods.

The four curves in Fig. 1 for August 21 show that a minimum oxygen concentration of 7.5 mg/l was recorded for the 0.8 m. electrode at 6:00 a. m. and a maximum of 8.9 mg/l at 1:00 p. m., representing an increase of 1.4 mg/l at that depth during this period of time; the maximum, however, was only 95.6

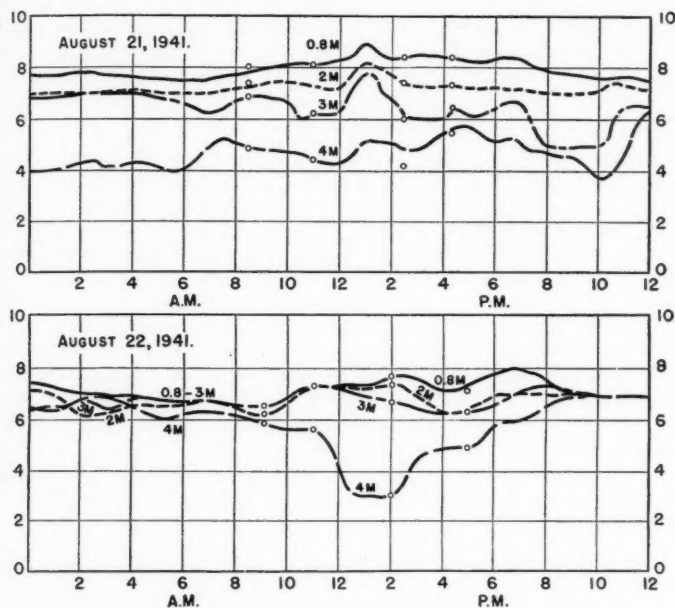


Fig. 1. Continuous records obtained with four dropping mercury electrodes which show the amount of dissolved oxygen in the 0-4 m. stratum of Little John Lake on August 21-22, 1941. The four sets of circles shown on the curves for each day represent the results of check determinations of oxygen made by the titration method. The vertical scale represents the number of milligrams of oxygen per liter of water and the horizontal scale shows the hours of the day.

per cent of saturation. At 2 m. the minimum was 7.0 mg/l at 6:00 a. m. and 8.15 mg/l at 1:00 p. m., an increase of 1.15 mg/l; the minimum at 3 m. was 6.3 and the maximum 7.8 mg/l, representing a gain of 1.5 mg/l at that depth. At 4 m. the minimum was 4.0 mg/l and the maximum 5.8 mg/l, an increase of 1.8 mg/l. Thus the average increase in oxygen for the 0-4 m. stratum during the day was 1.46 mg/l, or 1460 mg/m<sup>3</sup>. The total volume of water in the stratum is 2,115,700 m<sup>3</sup>, so that the mean increase in oxygen amounted to 3089 kg. for the entire lake, or 46 kg/ha. This quantity represents the net gain and does not include the oxygen consumed by the chlorophyll-bearing organisms in their own metabolic activities, nor that which was used by the zooplankton, the large aquatic plants and large aquatic animals, nor that which was consumed in the decomposition of organic matter. The glucose equivalent of this net gain of 46 kg/ha of oxygen is 24.5 kg/ha, or 22 lb/a.

Owing to the scarcity of oxygen in the lower water of Little John Lake in early August, the variations in the amount of this gas at 4 m. were so irregular

that this depth was omitted from the computations for oxygen production; thus only the results in the 0.3 m. stratum have been taken into consideration. Computing the readings of the dropping mercury electrodes for the 0.3 m. layer gives a yield of 33.3 kg/ha/da for the oxygen production on August 21, which is equivalent to 17.7 kg/ha/da of glucose.

With respect to the quantitative exchange of oxygen at the air-water interface on August 21, it may be said that the amount of this gas was well below the saturation point on that day. In the upper meter of water for example, the amount varied from 85.2 per cent of saturation in the morning to 95.6 per cent at 1:00 p. m., the maximum point in the curve, and then declined to 90.7 per cent at 4:20 p. m. Thus no loss of oxygen to the air should have taken place. Likewise it was a fairly calm day so that there was little agitation of the water by the wind to aid in the absorption of oxygen from the air and the coefficient of diffusion of this gas into water is so low that very little oxygen could have been acquired by the water through this process during the day. Furthermore the well defined peaks in the curves at 1:00 p. m. indicate that the accumulation of the oxygen was due to increased photosynthetic activities during the middle of the day rather than to absorption from the air. Even when the upper water was greatly disturbed by stronger winds during the following days, the amount of oxygen still remained well below the saturation point.

TABLE 2.—Results obtained in chemical analyses of the water of Little John Lake, expressed in milligrams per liter. Most of them are the means of two to five determinations which were made in different years.

Depth, meters	Bound CO <sub>2</sub>	Nitrogen		NO <sub>3</sub>	Phosphorus		
		NH <sub>3</sub>	Org. N		Soluble	Organic	Total
0	18.0	0.042	0.516	0.014	0.007	0.014	0.021
4	18.0	.....	.....	.....	0.008	0.020	0.028
6	18.0	0.188	0.523	0.015	0.008	0.022	0.030

	SiO <sub>2</sub>	Fe	Mn	Ca	Mg	Cl	SO <sub>4</sub>	Residue
0	3.4	0.27	0.12	12.2	3.2	0.7	3.3	56.7
4	3.4	0.43	0.13	12.4	3.5	.....	.....	.....
6	4.5	0.71	0.23	12.4	3.7	0.7	.....	58.6

The 3 m. and 4 m. curves in the late afternoon of August 21 show marked changes in the oxygen content at those depths; these changes were due to the shifts in the lower water produced by a rising wind which came on at that time. By midnight the wind became strong enough to produce an almost complete mixing of the water of the 0.4 m. stratum. The brisk wind continued the mixing of the upper water during the night and early hours of August 22 as shown in the lower part of Fig. 1, but a decrease in the strength of the wind during the day permitted the water at 4 m. to shift back to its former condition of low oxygen concentration. Again an increase in wind activity in the late afternoon and the early evening of August 22 disturbed the water throughout the 0.4 m. stratum so that the oxygen concentration became uni-



form at 6.8 mg/l, which was about 72.0 per cent of saturation. The circles shown on the curves for August 22 represent the titration results obtained on that day; they check closely with the readings obtained with the dropping mercury electrodes.

### Oxygen Titrations

During the month of August, four or more sets of samples covering the 0-4 m. stratum were taken for oxygen titrations on the same day. Usually they were obtained between 9:00 a. m. and 4:00 p. m., thus covering the most active photosynthetic time of the day. In general such observations were made on days when the lake was calm or when the water was disturbed only by light winds. These series of observations showed that the increase in oxygen in the 0-3 m. stratum ranged from 13 to 34 kg/ha/da, with a glucose equivalent of 7 to 18 kg/ha/da, depending upon the condition of the sky, the abundance of the phytoplankton and other factors. Oxygen determinations were made at 4 m. also, but the results at that depth were too irregular to be used in the above computations, especially during the first half of August.

These titration observations show that regular series of this kind, when taken frequently enough during the day, will give a general idea of the daily oxygen changes in a lake like Little John, from which rough approximations of the quantity of organic matter produced can be computed. They will represent the net gain in the oxygen content of the water, but they will not indicate the amount of oxygen consumed in respiration and decomposition. When taken at hourly intervals from sunrise to sunset, with half-hour periods during mid-day when photosynthesis reaches a maximum, such observations will give a general picture of the metabolic changes taking place in the lake during the daytime; these results, however, should be supplemented with series taken every two or three hours during the night when katabolism dominates the biological activities. A more complete picture is obtainable, of course, with dropping mercury electrodes when oxygen readings are recorded every two minutes both day and night. By either of these methods, it is necessary to suspend samples of water in the lake to determine the quantity of oxygen consumed.

### Oxygen Production

The upper part of Table 3 shows the mean chlorophyll content of the water and the general results for oxygen production in the 8 series of bottle samples suspended in Little John Lake on different dates and for different periods of time ranging from four hours to four days. It is based on the results obtained in the upper 3 m. of water, both for daily and hourly periods; for convenience the hourly rate of production has been carried out to three decimal places so that the smaller yields may be interpreted as grams instead of kilograms per hectare. It will be noted that two of the series remained suspended in the lake only four and 7 hours, respectively, while the other 6 remained one to four days.

As might be expected series No. 1 and No. 2 show the highest hourly rate

TABLE 3.—The upper part of this table shows the quantity of oxygen produced in Little John Lake in various periods of time. The samples were taken at different depths and suspended from the buoy at the same depths from which they were taken. The computations are based on the results obtained in the 0-3 m. stratum. The lower part of the table indicates the oxygen consumption in the black bottles. The series of samples have corresponding numbers in both parts of the table.

No.	Date, 1941	Hours	Chlorophyll, mean, mg/m <sup>3</sup>	Oxygen produced, kg/ha			Glucose equivalent, kg/ha/da
				Total	Per day	Per hour	
1	7/31	4	19.43	22.2	-----	5.550	-----
2	8/4	7	13.60	22.2	-----	3.171	-----
3	8/25-26	24	15.00	30.4	30.4	1.268	16.2
4	8/25-27	48	15.00	50.5	25.2	1.052	13.4
5	8/15-18	72	11.65	52.4	17.5	0.728	9.3
6	8/18/21	72	12.80	56.6	18.9	0.786	10.1
7	8/5-9	96	7.53	95.5	23.9	0.995	12.7
8	8/11-15	96	10.20	50.1	12.5	0.521	8.0

No.	Hours	Oxygen consumed, kg/ha			Per cent
		Total	Per day	Per hour	
1	4	10.8	-----	2.700	48.6
2	7	11.1	-----	1.590	50.0
3	24	17.0	17.0	0.708	55.8
4	48	24.8	12.4	0.517	49.1
5	72	37.1	12.4	0.515	70.7
6	72	39.1	13.0	0.542	69.0
7	96	65.1	16.3	0.678	68.1
8	96	32.2	8.0	0.335	64.0

of oxygen production because they were left in the lake only during the day-time when there was sufficient subsurface solar radiation for the process of photosynthesis. The hourly production of the 7-hour series was only 57 per cent as large as that of the 4-hour series; this difference in yield was due mainly to the light conditions that prevailed on the two days. The total yield, however, was the same on the two dates, namely 22.2 kg/ha.

The daily oxygen production of the other series (Nos. 3-8) ranged from a minimum of 12.5 kg/ha for the August 11-15 period (No. 8) to a maximum of 30.4 kg/ha for the August 25-26 series (No. 3). The highest hourly rate of oxygen production was noted in No. 3 and No. 4 which were suspended in the lake for only one and two days respectively; their average hourly yield was 1.16 kg/ha, while that of the other four series, which were suspended in the lake for three and four days, was 0.76 kg/ha, or only 65 per cent as large. The lowest yield (No. 8) was found in the series which began on the morning of August 11 just after a heavy rain storm on the previous night; thus the dilution of the lake water with rain water and the increased cloudiness following the storm, as well as other environmental factors, appeared to interfere with the photosynthetic activities of the phytoplankton.

The mean quantity of oxygen produced daily by the 6 series suspended for

one to four days was 21.4 kg/ha, equivalent to 11.4 kg/ha of glucose. These sets of samples were well distributed through August and they covered 16 of the 31 days of the month, so that they may be regarded as representing the general oxygen production conditions during that time. Calculated on this basis the total oxygen production in the 0.3 m. stratum for the 31 days amounted to 663 kg/ha, with a glucose equivalent of 353 kg/ha, or 315 lb/a. Plankton samples taken as early in the year as April 26 and May 8 yielded as many phytoplankton organisms as those taken in June, July and August, while those obtained in late August showed no evidence of a marked decline either in numbers or in photosynthetic activity at that time; thus it seems safe to extend the August situation to the month of September too. Such extensions of time and activities to the other months would include the five warmer months of the year, namely May to September, inclusive. If the August rate of production is maintained during these five months, the oxygen yield for the 153 days would amount to 3274 kg/ha, or 1745 kg/ha of glucose; this is equivalent to 1556 pounds of glucose per acre.

The relation of the oxygen production, or more specifically the glucose production, to the mean standing crop of centrifuge plankton may now be considered. The mean quantity of dry organic matter in the standing crop of plankton in the 0.3 m. zone of the 5 series of catches represented in Table 4 amounts to 54.0 kg/ha. Thus a glucose production of 353 kg/ha for the month of August would be 6.5 times as large as the average standing crop of centrifuge plankton. That is, the glucose production during August would provide fundamental organic matter for a little more than a six-fold turnover of the standing crop of plankton. Applying the same method of computation to the May-September yield of glucose amounting to 1745 kg/ha would give a yield about 32 times as large as the average standing crop of centrifuge plankton. If one takes into account the quantity of oxygen consumed in respiration and decomposition on the 50 per cent basis, which would be equal to half the amount of glucose manufactured in the photosynthetic process, then the net yield of this organic material would be a little more than three times the standing crop of centrifuge plankton for August and 16 times that of the May-September period.

During the other 7 months of the year, photosynthesis proceeds at a slower pace due to the lower temperature of the water and the less favorable light conditions resulting from the lower altitude of the sun. The lake is covered with ice from about the middle of November to the middle of April, or approximately 5 months each year, so that the ice and snow greatly reduce the sub-surface light intensity during this time; no attempt has yet been made to determine the rate of photosynthesis during this season. In spring and autumn there is a complete circulation of the water of Little John Lake and at these times the entire body of water is brought to the surface from time to time where light as well as nutritive conditions are favorable for the photosynthetic activities of the phytoplankton. The autumn circulation extends from about mid-September to mid-November and the vernal one from mid-April to mid-May or later. These two periods of more favorable conditions for photosynthe-

sis make up, in part at least, for the minimum temperature and light conditions in winter.

### Oxygen Consumption

As already indicated the black bottle samples show the amount and rate of oxygen consumption of the microscopic plants and animals found in the water and also the amount used in the process of decomposition. It is shown by the difference in the oxygen content of the original water with which the black bottles were filled and the final oxygen content after the bottles have been suspended in the lake. Thus it applies only to the microscopic forms in the water and does not include the oxygen used for respiration by the large aquatic plants and the larger animals, such as insect larvae, worms, mollusks and fish.

A summary of the results obtained in the 8 series of experiments with the black bottles is given in the second part of Table 3; the series numbers correspond to those given in the first part of this table. It is interesting to note that the maximum hourly consumption of oxygen was found in series No. 1 which was suspended in the lake for only four hours; No. 2, the 7-hour series, was second and No. 3, the 24-hour series, ranked third. This is the same order as indicated in the first part of the table for the highest hourly rate of oxygen production. The other 5 series were well below these three in their hourly rate of oxygen consumption. The average consumption of the first three series was 1.666 kg/ha/hr, while that of the other 5 series was 0.517 kg/ha/hr, or less than one-third as much. This seems to suggest that the oxygen consumption became stabilized at a basic rate during the second day and remained fairly constant up to the end of the fourth day, which was the maximum length of time used in the experiments. Thus a higher rate of oxygen consumption was correlated with a higher rate of oxygen production, indicating a greater physiological demand for oxygen by the phytoplankton when photosynthesis is in progress. At night when light is not available for photosynthesis, the organisms consume oxygen at what may be termed their basic metabolism rate.

The percentage column in the second part of Table 3 shows that oxygen consumption in the first four series of samples was only about 50 per cent of the quantity produced; in other words the ratio of production to consumption was 2:1. In the four series extending over three to four days, the percentage of oxygen consumption amounted to 64 to 71 per cent, with a mean of 68 per cent, which gives a ratio of 1.4:1. The oxygen consumption in the black bottles is probably greater than in the lake itself because it has been found that putting lake water in bottles stimulates the growth of the aquatic bacteria. Fred, Wilson and Davenport (1924) reported a ten-fold to twenty-fold increase in the number of bacteria in bottled water from Lake Mendota in a period of 8 days, even when the bottles were anchored at the same depths from which the water was taken. Stark, Stadler and McCoy (1938) also found a marked increase in the number of bacteria in lake water stored in bottles; they attributed the increase in numbers to the accumulation of organic matter on the inner surface of the bottle which provided a more suitable concentration of nutrient material for the growth of the bacteria. Similar results were ob-

tained by ZoBell and Anderson (1936) with stored sea water. The observations of these investigators together with the results obtained in Little John Lake, indicate that the bottle method for oxygen production and consumption must be used with caution. The present data seem to show that the sample bottles should not be left in a lake more than 48 hours in order to obtain the most reliable results, especially in summer when the temperature of the water is high: the duration of the suspension will also depend to a certain extent on the abundance of the phytoplankton in the water used for the samples.

The mean quantity of oxygen consumed in the 6 series which remained in the lake 24 to 96 hours was 13.2 kg/ha/da, with a glucose equivalent of 7 kg/ha/da. This amount is to be compared with the mean oxygen production of the same series amounting to 21.4 kg/ha/da, which represents a glucose equivalent of 11.4 kg/ha/da. Thus the oxygen consumption in these 6 series amounted to 61.4 per cent of the oxygen production. As previously noted the net gain in the oxygen content of the water as shown by the dropping mercury electrodes for the 0-3 m. stratum was 33.3 kg/ha/da, or 17.7 kg/ha/da of glucose; but this amount does not take into account the quantity of oxygen consumed. Using the short period rate of oxygen consumption shown in the experimental series (No. 1-4, inclusive), namely 50 per cent, would give a total yield of 66.6 kg/ha/da of oxygen for the electrode results of August 21, which is equivalent to 35.4 kg/ha/da of glucose.

The carbohydrate manufactured by the phytoplankton is utilized by these organisms in three ways: (1) some of it is oxidized by them in their metabolic activities, (2) some of it is stored as a reserve for future use, and (3) part of it is combined with nitrogen and several other elements to form protoplasm for growth and for the formation of new individuals to replace those that have completed their life span or to increase the total number of organisms. The utilization of the reserve material was well illustrated by a series of experiments on August 6-7, a cloudy day, when respiration and decomposition used up about two and a half times as much oxygen as was produced in photosynthesis.

### Photosynthetic Capacity of Surface Water

In order to test the photosynthetic capacity of the algae in the surface stratum of Little John Lake under different transparency conditions, four series of samples of this water were suspended at one meter intervals in the 0-6 m. stratum of Trout Lake; one series remained in Trout Lake 5 hours, one 7 hours and two 24 hours. At the time the transparency of the water was 1.8 m. in Little John and 4.5 m. in Trout. In the 5-hour series the oxygen yield in the 0-3 m. zone amounted to 4.68 kg/ha/hr, in the 7-hour series 4.12 kg/ha/hr and in the two 24-hour series 1.00 and 1.67 kg/ha/hr, respectively.

The mean yield of the Little John surface samples suspended in the upper 3 m. of Trout Lake was 4.40 kg/ha/hr of oxygen in the 5-hour and 7-hour series as compared with 4.36 kg/ha/hr in the 4-hour and 7-hour series suspended in Little John Lake. Likewise the mean of the two 24-hour series in Trout was substantially the same as that of the one 24-hour series suspended in

Little John, namely 1.33 kg/ha/hr in the former and 1.27 kg/ha/hr in the latter. These slight differences in oxygen yields in the two lakes indicate that transparency of the water had little or no effect on oxygen production in the upper 3 m. under the conditions of the experiments. The results also show that the photosynthetic capacity of the phytoplankton at 2 m. and 3 m. in Little John Lake was substantially the same as that at the surface since samples from these two depths were used in the Little John experiments. The average oxygen consumption was about 50 per cent greater in the samples suspended in Little John than in those suspended in Trout. While oxygen production took place at 6 m. in Trout Lake in the four series of samples, the maximum production was noted either at 2 m. or 3 m. In the two 24-hour series in Trout Lake, the 6 m. samples marked the compensation point; that is, the amount of oxygen produced was the same as the quantity consumed.

### Seasonal Changes in Oxygen Content

When the phytoplankton is actively carrying on photosynthesis in July and early August, the upper water of Little John Lake may become supersaturated with oxygen. Table 1 shows excesses ranging from 20 to 67 per cent at the different depths; on August 2, for example, the 0-3 m. stratum contained 17,554 kg. of oxygen (261 kg/ha), which was 3146 kg. (47 kg/ha) in excess of the amount required to saturate the water. An excess of 45 kg/ha was found in the afternoon of August 4 and one of 32 kg/ha on August 5. These quantities of excess oxygen coincided with a period of relatively calm weather when the water of the epilimnion was not greatly disturbed by wind; hence the loss of excess oxygen to the atmosphere was comparatively small.

An oxygen deficit was found in the lower water when the upper water had an excess amount; on August 2 the 3-6 m. stratum had a deficiency of 5713 kg., so that there was a net deficit of 2567 kg. in the entire lake at that time. In the series of samples taken at 8:30 a. m. on August 22, instead of an excess of oxygen in the 0-3 m. stratum, there was a deficit of 5030 kg. as compared with an excess of 3146 kg. just 20 days earlier; in fact the excess in the 0-3 m. stratum had changed to a small deficit by August 11. The deficit for the entire lake reached 7892 kg. on August 22, or an average of 107 kg/ha. This was the largest deficiency noted in the various observations. The deficiency was due in part to the cooling of the upper water which increased its capacity for oxygen and to the stronger winds in the latter part of August which caused some of the lower water with its very low oxygen content to be mixed with the upper water at that time. The latter represented the first step in the fall overturn and mixing of the water of the entire lake. The bottle samples taken the latter part of August showed that the photosynthetic capacity of the phytoplankton was substantially the same as it had been earlier in the season.

### Chlorophyll and Plankton

Determinations of the chlorophyll content of the water were made from time to time for purposes of comparison with the plankton and the rate of

oxygen production. In five series both chlorophyll and plankton samples were taken on the same day. The results are given in Table 4; the oxygen determinations are included in the table also. The quantity of chlorophyll ranged from a minimum of 5.8 mg/m<sup>3</sup> at 0.8 m. on August 4 to a maximum of 28.2 mg/m<sup>3</sup> at 3 m. on the same date. The second largest amount was 27.0 mg/m<sup>3</sup> found at 2 m. on July 31. Surface readings were not taken on July 31 and August 4, but they were obtained on the other dates as shown in the table.

The quantity of dry organic matter in the centrifuge plankton varied from a minimum of 1160 mg/m<sup>3</sup> at 2 m. on August 4 to a maximum of 3860 mg/m<sup>3</sup> at 3 m. on July 31. The percentage of chlorophyll in the dry organic matter of the centrifuge plankton is given in the last column of Table 4; the minimum was 0.39 per cent at 0.8 m. on August 15 and the maximum 1.06 per cent at 3 m. on August 4. Only three samples contained more than one per cent of chlorophyll. Manning and R. E. Juday (1941) record 17 centrifuge plankton samples from Scaffold Lake which yielded more than one per cent of chlorophyll and 17 from Nebish with 1.05 to 4.87 per cent. In Little Rock Lake the percentages above one per cent ranged from 1.27 to 5.91 and two from Muskellunge contained 1.38 and 3.18 per cent. With respect to the highest readings, they state that "it is probable that the chlorophyll content of algal cells is seldom much higher than this figure," namely 5.0 per cent. Their minimal percentages were found in Crystal and Trout lakes, 0.09 per

TABLE 4. The quantity and the percentage of chlorophyll in the dry organic matter of the centrifuge plankton.

Date, 1941	Hour	Depth, meters	Temp. °C	Oxygen mg/l	Chlorophyll, mg/m <sup>3</sup>	Plankton, mg/m <sup>3</sup>	Per cent chlorophyll
July 31	9:00 a.m.	0.8	26.0	9.2	7.5	1780	0.42
		2	24.2	9.4	27.0	2670	1.01
		3	20.7	10.0	23.8	3860	0.62
		4	18.5	0.5	10.0	1680	0.60
Aug. 4	9:20 a.m.	0.8	25.8	8.7	5.8	1450	0.40
		2	23.8	8.6	6.8	1160	0.59
		3	20.7	10.2	28.2	2650	1.06
		4	18.5	0.3	14.8	1420	1.04
Aug. 15	9:55 a.m.	0	21.5	7.1	12.7	2435	0.52
		0.8	21.5	7.1	12.4	3190	0.39
		2	21.5	7.0	12.2	1680	0.73
		3	21.2	6.2	9.3	1860	0.50
	9:30	4	20.8	4.4	9.1	1420	0.64
Aug. 18	9:20 a.m.	0	20.5	7.4	16.7	2320	0.72
		0.8	20.5	7.4	11.3	2720	0.42
		2	20.5	7.4	14.3	2050	0.75
		3	20.5	7.3	8.8	1780	0.49
	9:10	4	20.5	7.4	9.3	1550	0.60
Aug. 25	8:20 a.m.	0	20.5	7.6	17.1	2170	0.79
		0.8	20.5	7.6	14.3	1960	0.73
		2	20.5	7.6	14.1	1880	0.75
		3	20.3	7.0	14.5	1770	0.82
	8:00	4	20.0	5.4	11.5	1740	0.64



cent in the former and 0.11 per cent in the latter. In the majority of their samples the chlorophyll content ranged from 0.2 to 0.8 per cent of the organic matter.

In view of the wide range in the percentage of chlorophyll in these centrifuge catches, this pigment can hardly be regarded as a good index of the phytoplankton which is the major constituent of this material. Riley (1938) found a close correlation between chlorophyll and phytoplankton in the epilimnion but not in the hypolimnion. One of 6 series in Little John did not show a good correlation between chlorophyll and phytoplankton in the epilimnion. The chlorophyll content of the phytoplankton may be affected by several factors, such as the different kinds of organisms represented, their age and physiological status and their relation to environmental factors, for example light and nutrients. The variations in percentage may also be due, in part at least, to differences in the proportion of phytoplankton and zooplankton in the catches and to changes in the organic detritus constituent of the material.

Observations on 25 lakes show that the zooplankton furnishes from one per cent to about 25 per cent of the organic matter found in the centrifuge plankton. As might be expected the percentage of zooplankton varies in the different lakes and also in the same lake at different times. Riley (1941) states that total plant pigments are a better index of phytoplankton than chlorophyll. This would be true especially where the phytoplankton contains large numbers of organisms that are well supplied with carotinoid pigments, such as diatoms. Dutton and Manning (1941) found evidence for carotinoid-sensitized photosynthesis in the diatom *Nitzschia*, so that these pigments need to be taken into account in connection with the problem of oxygen production. On the other hand the data presented in Table 3 show that there is a significant correlation between chlorophyll and oxygen production in Little John Lake without regard to the carotinoid pigments present. That is, the correlation coefficient between the chlorophyll content of the water and the hourly oxygen production in the 8 series listed in the table is 0.736 which is large enough to have considerable significance.

#### Phytoplankton Constituents

Numerical data for the phytoplankton are given in Table 5, which indicates the number of organisms per milliliter of water. Blue-greens were the dominant forms; they consisted chiefly of representatives of the following genera: *Anabaena*, *Aphanocapsa*, *Chroococcus*, *Coelosphaerium*, *Merismopedia* and *Microcystis*. Some other genera of this group appeared in the catches occasionally, but they were not abundant enough to play any appreciable rôle in the phytoplankton community. The green algae were represented by small numbers as shown in the table; *Scenedesmus* and *Staurastrum* were found most frequently. The diatoms ranked second in abundance and they belonged chiefly to the genera *Fragilaria* and *Synedra*. The average number of phytoplankters in the 6 series of catches represented in Table 5 showed less than a two-fold range in variation. A maximum average of 4730 cells and colonies per milliliter was

found in the 0.4 m. stratum in the series taken on July 31, while the mean for the 0.3 m. stratum, which was used in the computations of the oxygen production, was 5750 per milliliter. The minimum average in the 0.3 m. layer was noted in the series of August 25, namely 2650 per milliliter and 2595 per milliliter in the 0.4 m. zone.

There was a significant correlation between the chlorophyll content of the water and the number of phytoplankton organisms found in the 0.3 m. catches of four of the 6 series given in Table 5. The series taken on August 18 has a correlation coefficient of 0.138 which is too low to be significant; complete data on chlorophyll were not obtained on August 11, so the correlation for that series cannot be computed. The mean correlation coefficient for the other four series is 0.882 which is large enough to be significant. In these four sets of samples the correlation is close enough to permit using the chlorophyll as an index of the phytoplankton, but the low correlation coefficient of the catches taken on August 18 shows that the chlorophyll cannot be relied on in all cases.

The relation between chlorophyll and the number of phytoplankters is shown graphically in Fig. 2. In the samples taken on July 31, there is a close

TABLE 5.—Number of cells and colonies of phytoplankton organisms per milliliter of water found at different depths in Little John Lake.

1941 Date,	Depth, meters	greens Blue-	Greens	Diatoms	Flagel- lates	Total
July 31	0.8	4048	9	121	11	4189
	2	5651	9	121	11	6136
	3	6695	17	208	9	6929
	4	1272	0	216	173	1661
Aug. 4	0.8	2604	0	43	0	2647
	2	4585	0	17	0	4602
	3	5977	0	26	43	6046
	4	2318	52	130	0	2500
Aug. 11	0.8	3192	17	0	0	3218
	2	1540	0	17	17	1574
	3	3408	17	9	26	3460
	4	2578	0	35	1220	3833
Aug. 15	0	7162	26	61	9	7258
	0.8	4489	43	78	9	4619
	2	4965	0	69	69	5103
	3	2586	26	52	35	2699
	4	2578	17	52	17	2664
Aug. 18	0	3053	78	121	9	3261
	0.8	4437	17	104	26	4584
	2	4732	112	35	9	4888
	3	2647	122	156	138	3063
	4	3668	26	104	147	3945
Aug. 25	0	4057	26	69	9	4161
	0.8	2517	17	130	9	2673
	2	1401	35	424	9	1869
	3	1488	9	415	26	1918
	4	1496	9	840	9	2354

correlation between the high chlorophyll content and the large number of phytoplankters at 2 m. and 3 m., but it is not so evident in the series taken on August 15, especially at the surface. Figure 3 illustrates the relation between chlorophyll and phytoplankton, as well as their relation to the dissolved oxygen. The correlation coefficient between chlorophyll and phytoplankton is too small to be significant as indicated in the previous paragraph.

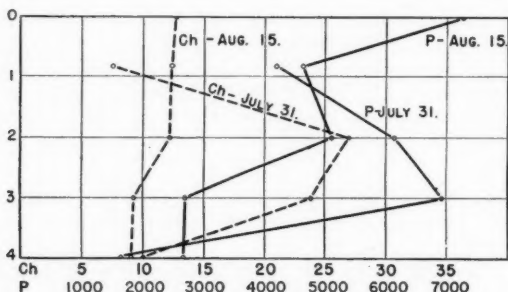


Fig. 2. The amount of chlorophyll (Ch) at different depths and the number of phytoplankters (P). The vertical scale shows the depth in meters; the upper horizontal scale indicates the number of milligrams of chlorophyll per cubic meter and the lower one the number of cells and colonies of phytoplankton per milliliter of water.

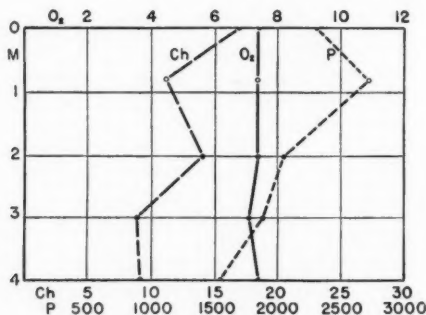


Fig. 3. The vertical distribution of the chlorophyll, the phytoplankton and the dissolved oxygen on August 18, 1941. The vertical scale shows the depth in meters. The horizontal scale at the top of the diagram indicates the quantity of dissolved oxygen in milligrams per liter; the upper horizontal scale at the bottom of the diagram indicates the amount of chlorophyll (Ch) per cubic meter and the lower one the number of phytoplankton organisms (P) per milliliter of water.

### Discussion

The production of primary foodstuffs in lakes by chlorophyll-bearing organisms is a complex problem because so many physical, chemical and biological factors are involved in the manufacturing process. Many phases of this complex problem have been investigated by limnologists, but so far very little work has been done on the determination of the actual amount of organic material photosynthesized by these organisms and the rate at which it is produced. Thus it has been necessary to depend on estimates, perhaps it would be better to say guesses, based on meager data to obtain a general idea of the monthly or annual yield of organic matter by various types of lakes. This is true despite the fact that these organic substances are such vital factors in the housekeeping activities of a lake. The annual crop of large aquatic plants has been determined for a few lakes, while the standing crop of phytoplankton has been studied in many lakes, but very little information is available concerning the turnover in this stock of microscopic life and the quantity of it that is produced during the course of a month or a year.

Speaking generally the strictly aquatic animal life of a lake is dependent primarily on the fundamental foodstuffs produced by the aquatic plants and there is such a close relation between these two groups of organisms that there seems to be a definite ratio of the one to the other (Juday 1943). In the summer standing crop of two soft water lakes, the ratio of plants to animals was found to be 6.3:1; excluding the fish the ratio became 7.5:1, while in one hard water lake it was 12:1 and in another 22:1, excluding the fish.

The first attempts to enlarge our knowledge of the production of organic matter in Wisconsin lakes consisted of suspending pure cultures of algae at different depths for various periods of time and determining their amounts and rates of oxygen production (Schomer and Juday 1935; Curtis and Juday 1937; Manning, Juday and Wolf 1938). The results of these experiments, however, did not throw much light on the actual production of organic matter in the lake itself because the algae that had to be used were limited to a few forms that were rarely represented in the phytoplankton; all attempts to culture the common and more abundant forms of plankton algae failed. On the other hand a certain amount of valuable information was obtained with the cultures. They showed the effects of color and transparency of the water on the process of photosynthesis, and depths to which photosynthesis extends in different types of lakes, the depths of maximum oxygen production, the total amount and rate of oxygen production and the ratio of the oxygen production to the total number of cells in the various suspensions. For the most part filtered lake water was used in making up the algal suspensions so that the experiments simulated natural conditions to that extent.

The next step in this field of investigation was taken by Kozminski (1938) who studied the chlorophyll content and its vertical distribution in several Wisconsin lakes. While he did not make any observations on the photosynthetic capacity of the chlorophyll, his investigations led to a more extended

study of the problem by Manning and R. E. Juday (1941). They studied the chlorophyll content of 8 lakes during the summers of 1938 and 1939, its vertical distribution, and its photosynthetic capacity by suspending samples in Trout Lake for periods of one to 9 hours, depending upon the abundance of the phytoplankton in the various samples. In this way they established the maximum rate of oxygen production and then used the oxygen data for the computation of the maximum rate of photosynthesis of epilimnion waters as a function of their chlorophyll content. At optimal light intensity the average capacity was found to be seven milligrams of oxygen produced per milligram of chlorophyll per hour; this corresponded to a reduction of one molecule of carbon dioxide by one molecule of chlorophyll every 18 seconds. Using a clear day on August 1 as a basis of calculation, the highest production of organic matter was equivalent to 44 kg/ha/da of glucose in Scaffold Lake and the lowest 14 kg/ha/da in Helmet Lake. These results fall within the maximum and minimum ranges observed in Little John Lake during the month of August.

Heinrich (1934) found the oxygen production in the upper 5 m. of Jagersee amounted to 0.03 mg/l/da in winter and 1.3 mg/l/da in summer; the oxygen consumed was 0.06 mg/l/da in winter and 0.24 mg/l/da in summer. Of the total production of organic matter amounting to 1300 gr/m<sup>2</sup>, 20 per cent was used in the destructive metabolism of the plankton organisms and 80 per cent in constructive metabolism. This represents a small percentage of oxygen consumption.

Winberg (1937a, 1937b) studied the oxygen production and consumption in four experimental fish ponds and in 11 small lakes. At the surface of the fish ponds, the maximum oxygen production was 4.85 mg/l/da on August 20 and the corresponding oxygen consumption was 3.33 mg/l/da; at the bottom of the ponds, the maximum production was 2.61 mg/l/da with a consumption of 1.45 mg/l/da. In the small lakes, the maximum production was 3.67 mg/l/da at the surface of one. None of the lakes exceeded 3 m. in depth and the oxygen content of all except one ranged from 74 to 90 per cent of saturation. In comparison with Winberg's results, the maximum oxygen production at the surface of Little John Lake was 2.46 mg/l/da.

Riley (1940) investigated the oxygen production and consumption of Linsley Pond in Connecticut from September 1937 to June 1938. The arithmetic means of his 13 series of samples show an oxygen production of 1.065 mg/l/wk and an oxygen consumption of 1.359 mg/l/wk; thus the consumption exceeded production by a little more than 27 per cent. Riley states that the sets of samples were not taken at equal intervals of time so that the arithmetic mean is probably not as accurate as the planimetric means of the seasonal curves; according to the planimetric method, the mean gross production on a glucose basis is given as 0.089 mg/cm<sup>2</sup>/da, or 8.9 kg/ha/da. This is substantially the same as the glucose production of the 3-day series of samples in the 0-3 m. stratum of Little John Lake on August 15-18 (No. 5 in Table 3), but it is larger than the 4-day series taken on August 11-14 (No. 8). The mean of the

6 Little John series is 11.6 kg/ha/da, which is somewhat larger than the mean for Linsley Pond.

Various factors must be taken into consideration in making a comparison of the results obtained on these two lakes. The Linsley observations include the winter season when temperature and light conditions are unfavorable for photosynthesis; however, only three sets of observations were taken in winter, one in December and two in January. The other 10 were obtained in autumn, spring and early summer when the standing crop of phytoplankton is usually larger than in mid-summer. Linsley is deeper than Little John and light conditions in the deeper strata would not be so favorable for photosynthesis even in summer because solar radiation is cut off rapidly by lake waters thus leaving only small amounts of it to energize the photosynthetic process in the deeper water.

While a certain amount of oxygen production was found at 13 m. in Linsley, it was only about half as large as that at 2 m. The number of phytoplankters was somewhat larger in Linsley than in Little John, but the mean chlorophyll content of the water was not very different in the two lakes, namely 13.6 mg/m<sup>3</sup> in the former and 12.4 mg/m<sup>3</sup> in the latter. In Linsley the oxygen consumption exceeded the oxygen production below 2 m. and the same was true of Little John below 3 m. Substantially no dissolved oxygen was found below 4 m. in Little John in late July and early August. Thus the metabolic activities of the phytoplankton are spread out through a depth of 13 m. in Linsley Pond, while they are concentrated in the upper 3 m. of Little John Lake in summer.

### Summary

1. The photosynthetic activities of the phytoplankton of Little John Lake were studied by means of dropping mercury electrodes and by bottle samples anchored in the lake at different depths and for different periods of time.

2. The mean chlorophyll content of the water fell between 7.5 and 19.4 mg/m<sup>3</sup>. The chlorophyll constituted from 0.39 per cent to 1.06 per cent of the dry organic matter in the centrifuge plankton. In four out of six series of samples, the quantity of chlorophyll was closely correlated with the number of phytoplankters.

3. The oxygen production of the phytoplankton varied from a minimum of 12.5 kg/ha/da to a maximum of 66 kg/ha/da, with glucose equivalents of 8 and 35 kg/ha/da, respectively. Total oxygen production from May to September, inclusive, is estimated at 3274 kg/ha, equivalent to 1745 kg/ha of glucose; this was 32 times the average standing crop of centrifuge plankton in August. A significant correlation was found between chlorophyll content of the water and the hourly rate of oxygen production.

4. The quantity of oxygen consumed ranged from a minimum of 8 kg/ha/da to a maximum of 33 kg/ha/da; the oxygen consumption varied from 48 per cent to 71 per cent of the oxygen produced on clear and partly cloudy days,

but on a cloudy day the oxygen produced was only 42 per cent of that consumed.

5. As a result of the photosynthetic activities of the phytoplankton, the water of the 0-3 m. stratum became supersaturated with oxygen in late July and early August; the maximum excess was 67 per cent above the amount required for saturation which was found at 3 m. on August 5.

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## Some Observations on Epiphyllous Lichens in Northern Idaho

R. F. Daubenmire

Epiphytic bryophytes and lichens are common constituents of plant communities in temperate latitudes, but so far as the writer is aware the occurrence of the epiphyllous type of epiphyte at latitudes as high as the northern tier of the United States of America has not yet been reported. Apparently this is due only to the small size and rarity of the individuals, for the writer has found what appear to be nine species of lichens growing upon the foliage of coniferous trees in northern Idaho.

The collections upon which this report is based were obtained in forested ravines on the south slope of the Thatuna Range in Latah County, Idaho. In all cases the epiphylls were on trees growing in habitats where the climax forest, in the absence of cutting and burning, would be a nearly pure stand of *Thuja plicata*.

In September, 1941, an abundance of small lichens was discovered on the foliage (and twigs) of certain coniferous trees (Figs. 1 and 2), many of them growing upon foliage produced during the current year. Not only had they invaded the leaf surfaces and produced relatively mature thalli since the buds expanded in the spring, but many already bore fruiting structures. Such a rate of growth and maturation appears to be far more rapid than usual in lichens, for in a series of lichens studied by Fink,\* a minimal period of 4 to 8 years was necessary for the plants to become established and mature sufficiently to produce apothecia. The epiphylls in Idaho had accomplished as much within 3 to 4 months!

The foliage of six species of coniferous trees which grow intimately associated on this slope have been examined for epiphyllous lichens: western arborvitae (*Thuja plicata*), Douglas fir (*Pseudotsuga taxifolia*), grand fir (*Abies grandis*), Engelmann spruce (*Picea engelmannii*), western yew (*Taxus brevifolia*), and ponderosa pine (*Pinus ponderosa*). No lichens of any kind have yet been found on the needles of pine and spruce; among the other four species by far the best development of lichens is on the arborvitae. The only lichens observed on the needles of Douglas fir are thalli which became established on the twigs then extended out along the upper surface of the needles.

The superiority of arborvitae foliage as a habitat for epiphylls may possibly be attributed to three unique characteristics: (1) the scale-like form of the leaves which overlap to provide crevices in which anchorage is facilitated, (2) the roughness of the surface due to short peg-like papillae, one of which

\* Fink, B. The rate of growth and ecesis in lichens. *Mycologia* 9:138-158. 1917.

projects from each epidermal cell (These are not present on all leaves or on all parts of the same leaf.), and (3) a superficial film of scurfy material which is often produced by the leaves, especially in the immediate vicinity of the crevices. Frequently a coherent mass of scurf, hyphae and thallus can be picked out of these crevices, analogous to strips of sod which may be pulled from rock crevices in which grasses have become established. Most of the lichens found on *Thuja* appear to gain their initial foothold on the foliage by taking advantage of these crevices. The brownish scurf, which is copious on certain individual trees but entirely absent from others, provides a surface which can hold dust particles and in this way the condition of extreme nutrient deficiency, inherent to the needle-surface habitat, may be partially alleviated. Nevertheless, the problem of nutrient deficiency appears not to be of particular importance to these lichens, for those few individuals which become established upon the glossy surface of an *Abies* needle appear to develop about as rapidly as individuals of the same species growing upon *Thuja*. The reason for the complete absence of lichens on pine and spruce needles is not apparent, for the needles of these species are not so smooth and glossy as are those of *Abies*, and would seem to provide many more opportunities for disseminules to find lodgement.



Fig. 1. Epiphyllous lichens on *Thuja plicata*. Most of the plants including the apothecia near the center belong to *Teloschistes ramulosus*. A single apothecium of *Buellia* sp. appears near the middle of the second branch from the bottom on the right.

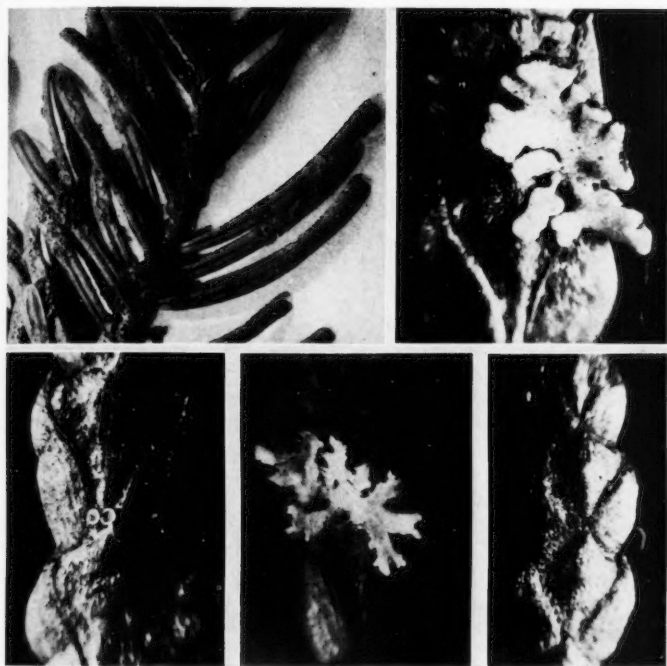


Fig. 2. Above left: mostly *Teloschistes ramulosus* on *Abies grandis*, but a large dark thallus of *Anaptychia* sp. covers a portion of the stem and adjacent leaf bases toward the bottom of the picture; Above right: *Parmelia physodes* on *Thuja*. Below, left to right: *Buellia* sp. on *Thuja*; *Physcia hispida* on *Thuja*; and *Lecideia* sp. on *Thuja*.

In September of 1942, the same area from which most of the 1941 collections were obtained was reexamined and it was found that practically no new epiphyllous plants had become established on the 1942 foliage. The fact that the early part of summer in 1941 was unusually wet (see Table 1) may well account for the greater success of establishment of the epiphylls during that

TABLE 1.—Departure, in inches, from the normal precipitation at Moscow, Idaho.

Month	1941	1942
April .....	+ 0.77	— 0.17
May .....	+ 2.52	+ 0.25
June .....	+ 2.08	+ 0.27
July .....	— 0.31	+ 0.16
August .....	+ 0.11	— 0.67

season. If the relative abundance of epiphylls is thus closely correlated with variations in precipitation, the epiphyllous habits of the lichens must have a decided cyclic rhythm. During the drier phases of climatic cycles these potentially epiphyllous lichens must be practically confined to bark or other surfaces which are less extreme habitats than leaf surfaces.

Little information has been gained as to the persistence of individuals once they have become established upon the leaf surfaces, but few plants are capable of maintaining their places for a year. Epiphylls may be found on foliage eight years old, but these individuals are not sufficiently larger than one-season-old plants to indicate that they are as old as their supporting leaves. Possibly the failure to persist may be attributed to the wedge-like action of ice formed when capillary films held under the thalli freeze and expand.

Undoubtedly the small size of these lichens is an important factor in their success, for relatively little photosynthate needs to be used in producing a vegetative body before the development of reproductive structures commences. Depending upon the species, the forms which were found vary from strictly microscopic size to individuals with thalli seven millimeters in length.

Certain epiphyllous lichens are known to be partially parasitic upon the leaves which support them. With the exception of *Amphiloma* sp., at least one specimen of each of the nine species considered in this report has been imbedded in paraffin and sectioned to discover possible evidences of parasitism. In no case was there observed a penetration of the tissues by the lichenous hyphae, nor the anatomy of the leaf beneath the lichen in any way abnormal. The lichens were characteristically anchored with organs composed of masses of rhizoids which take either of two forms. The attachment organ may be cord-like, expanding abruptly at the distal end to produce a thin disc, roughly circular in outline, which adheres to the cuticular surface. In other cases the hyphae take the form of a wedge-shaped plate which extends down vertically into (and completely fills) the crevices between the adjacent scale-like leaves of Thuja. In no cases have thalli been observed on the under side of leaves. Even where the crevices extend all the way from the upper to the lower surface of the Thuja foliage sprays, the anchoring hyphae fill the spaces completely but never extend beyond the confines of the crevice at its lower extremity.

Where branches are heavily infested with lichens, the photosynthetic function of the tree is undoubtedly curtailed to a great extent by the shading effect. A few cases were noted where as much as 50% of the total foliar surface on sheltered branches was covered with lichens, so that the foliage had a distinctly rusty appearance due to the predominance of the orange-colored *Teloschistes ramulosus*, but since this degree of cover is by no means common the sylval significance of these epiphyllous lichens would appear to be negligible.

A list of the lichens, which have been tentatively identified by Mr. George A. Llanos, together with the trees upon whose leaves they have been found growing is as follows. The letter A in parenthesis indicates that individuals

have been observed which produced apothecia during the same summer in which they invaded the leaf surfaces, and the letter S has the same meaning in connection with soredial bodies.

*Amphiloma* sp.—on grand fir and arborvitae.

*Anaptychia* sp. (A, S)—on grand fir and arborvitae.

*Buellia* sp. (A)—on arborvitae.

*Lecidea* sp. (A)—on grand fir and arborvitae.

*Parmelia physodes* (L.) Ach.—on arborvitae.

*Pertusaria* sp. (A)—on arborvitae.

*Physcia hispida* (Schreb.) Frege—on grand fir, yew, and arborvitae.

*Teloschistes* (*candelarius* var. *laciniosus*?) (A)—on arborvitae.

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## Comparison of Aquatic and Terrestrial Plants of *Isoetes Engelmanni* in the Mountain Lake, Virginia Area

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A species of *Isoetes*, classified as *I. Engelmanni* A. Br. by those who have collected it,<sup>2</sup> has been found in several stations in the Mountain Lake area, Giles Co., Virginia. It grows rooted in mud in the overflow of a spring below the Bear Cliff trail; in sphagnum in Hunters Branch near the Mountain Lake Biological station; along the banks of Little Stony Creek upstream from the Ashley home; and is found along the borders of and completely submerged in Mountain Lake.

*Isoetes Engelmanni* did not inhabit the lake in 1890 as is indicated in a letter received from Dr. J. H. Barnhart, in which he quotes the following passage from a report of a collecting trip in May and June of 1890 [Mem. Torrey Bot. Club 2 (2):34].

We explored the lake and its borders, but with the exception of a few plants of *Parnassia asarifolia* growing on old logs, and a few mosses in the water, of vegetable life there was none, nor much of animal life either, for the matter of that.

At present no information is available regarding the time when this species became an inhabitant of the lake; it must have been growing in the lake prior to the establishment of the Biological Station because it was seen in the lake about twenty years ago by those who examined the area for that purpose. It is safe to say now that *Isoetes Engelmanni* invaded the lake between 1890 and 1921.

Because of the marked diversity in the habitats in which this species of *Isoetes* is found at Mountain Lake, the question was raised as to whether or not any visible changes had occurred in the plants now growing submerged all the time. Both submerged and land plants were collected and compared in an effort to answer this question. Pfeiffer's (1922) description of *Isoetes Engelmanni* was used as a basis for the comparison, the results of which are shown in the accompanying chart.

Both aquatic and terrestrial plants in the Mountain Lake region differ from Pfeiffer's description in two characteristics. All of the Mountain Lake

<sup>1</sup> The writer wishes to thank Dr. Ivey F. Lewis for his helpful suggestions and for the fellowships at the Mountain Lake Biological Station which made this work possible, as well as Dr. R. B. Wiley and Dr. J. H. Barnhart who so kindly furnished information used here.

<sup>2</sup> Canby collected it in the Mountain Lake area in 1869 and 1889, and Massey and Carroll 1938 reported it from this area.

specimens have light tan colored megaspores—Pfeiffer's specimens have white megaspores; all of the Mountain Lake specimens have megaspores measuring  $390\mu$ —those of Pfeiffer's description measure 400-570 ( $615\mu$ ) in diameter. These variations exhibited by the Mountain Lake specimens are not of sufficient magnitude to be of diagnostic significance.

A comparison of the submerged and land plants of *Isoetes Engelmanni* at Mountain Lake discloses their striking similarity in many characteristics. Both have a two-lobed corm, numerous stomata, four peripheral strands in their leaves, leaves variable in length and number, oblong, unspotted sporangia, light tan megaspores, megaspores  $390\mu$  in diameter, megaspores distinctly marked with a honeycomb network of ridges, microspores  $24\mu$  in length and smooth to minutely roughened. The submerged plants have as many and as large stomata as the terrestrial plants have. The stomata of the aquatic plants are filled with gas bubbles indicating that the stomata are functioning. Cross sections were made of leaves from both habitats. The sections were cut at a point midway the length of the leaves and then were stained with Sudan III

TABLE 1.

Pfeiffer's description of <i>I. Engelmanni</i> .	Submerged specimens of <i>I. Engelmanni</i> from Mt. Lake, Virginia.	Terrestrial specimens of <i>I. Engelmanni</i> from Mt. Lake area.
Corm 2-lobed	Corm 2-lobed	Corm 2-lobed
Leaves 15-60 (100	Leaves 15-35	Leaves 20-40
Leaves 13-50 cm. long	Leaves 21-47 cm. long	Leaves 20-53 cm. long
Leaves light green	Leaves dark green	Leaves light green
Stomata numerous	Stomata numerous	Stomata numerous
Peripheral strands variable in number or none	Peripheral strands usually four	Peripheral strands usually four
Sporangia oblong, unspotted	Sporangia oblong, unspotted	Sporangia oblong, unspotted
Velum narrow	Velum $1/4$ - $3/4$ length of sporangium.	Velum $1/8$ - $2/5$ length of sporangium
Megaspores white	Megaspores light tan	Megaspores light tan
Megaspores 400-570 ( $615$ ) $\mu$ in diameter	Megaspores $390\mu$ in diameter	Megaspores $390\mu$ in diameter
Megaspores distinctly marked with honeycomb ridges	Megaspores distinctly marked with honeycomb ridges	Megaspores distinctly marked with honeycomb ridges
Microspores 21-30 $\mu$ (33)	Microspores usually $24\mu$	Microspores usually $24\mu$
Microspores smooth to minutely roughened	Microspores smooth to minutely roughened	Microspores smooth to minutely roughened



and chlorophyll, both specific stains for cuticle. A cuticle of the same thickness was found on the epidermis of all plants, aquatic and terrestrial alike. These observations are interesting because they are contrary to accepted opinions concerning stomata and cuticles of aquatic plants (Jeffrey 1917, Eames and MacDaniels, 1925).

However, Dr. Robert B. Wylie reported the following observations made during his work with aquatic plants (in lit.):

While I have done some work with aquatic plants, my interest has been primarily in the seed producing parts. I have often noted, however, that *Bidens Beckii* regularly produces, in water of proper depth, some entire leaves which may be provided with cuticle and stomata while still submerged. Later the flowers and upper leaves often emerge, pushed out of the water by stem elongation. In studying *Elodea* it was interesting to me to find that heavily cutinized pollen grains were produced several inches beneath the surface of the water. Evidently the production of a cuticle is not contingent upon free exposure to the outer air, though it may be under some circumstances, as in the case of the pollen grains, the modified wall might be exposed against gases imprisoned in the flower bud during later stages of development.

The only visible differences between the submerged and terrestrial plants are seen in the darker green color and a greater variety in the width of the velum of the aquatics. The latter characteristic is not sharply defined in the descriptions of this species. Pfeiffer (1922) calls the velum of *Isoetes Engelmanni* "narrow." Gray's Manual says that *I. Engelmanni* is "one fourth or less indusiate," variety *valida* is "one third to two thirds indusiate," and variety *fontana* has the "velum narrow." Since this character is so poorly delimited, the greater variation in width observed in the aquatics seems unimportant.

### Summary

Although the specimens of *Isoetes Engelmanni* growing in the Mountain Lake, Virginia area vary slightly from taxonomic descriptions of the species, the variations are not considered of sufficient magnitude to separate them as new entities.

Stomata of the same size and number as in the terrestrial plants are present in the submerged plants. They are in a functioning condition.

Contrary to common belief, the formation of the cuticle on the leaves of this species in the Mountain Lake area is not a direct response to exposure to the atmosphere; submerged specimens show a cuticle as well developed as that of terrestrial plants.

The plants growing in the lake retain essentially the same diagnostic characteristics as those found in nearby terrestrial habitats. The only visible differences are: the darker green color and greater variation in the width of the velum in the submerged plants. The latter is considered unimportant, since this character is not sharply defined in the available descriptions of the species.

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## The Genera of the Living Euphorbieae

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The purpose of this paper is to elucidate the genera which have been proposed in the tribe *Euphorbieae* of the family *Euphorbiaceae*. Fossil genera are excluded. The need for this study is evident when it is revealed that since 1753, the beginning date of modern botanical nomenclature, there has been no treatment of this subject which has attempted to identify accurately the many genera proposed as segregates of the genus *Euphorbia* L. This sweeping generalization may sound too bold, but it is true. Within one year, Miller (1754)<sup>1</sup> started the segregation of genera from *Euphorbia*. Ever since then genera have appeared more rapidly than they have been assimilated. The work of Boissier (1862) was the first adequate attempt at a monographic treatment of this group, but the multitudinous genera of Rafinesque were almost wholly unknown to Boissier. Pax (1891) and later Pax and K. Hoffmann (1931) made a general synopsis of the *Euphorbieae*, but many of the genera of Rafinesque and other authors were identified no further than that they belonged to the huge and complex genus *Euphorbia* L. There are even certain immediately practical considerations in this study. While workers of the caliber of Boissier, Jean Mueller ("Muell. Arg."), and F. Pax, who have studied the genus *Euphorbia* from a world-wide viewpoint, have preferred to keep the genus in its broad sense, some other workers, as Rafinesque, Haworth, Klotzsch & Garcke, Millspaugh, and particularly writers of local floras, as Small, have divided the genus *Euphorbia* into smaller genera of various sizes and degrees of homogeneity. It is particularly important that names used in floras should be at least nomenclaturally correct. Many of the genera described by Klotzsch & Garcke were anticipated by Rafinesque, yet writers of floras persist in using the later names. It is in the hope of elucidating these many genera and thus making a contribution to the understanding of botanical nomenclature that this paper is published. This basic bibliographic and taxonomic synopsis organizes and interprets the widely scattered material relating to these genera.

### PLAN OF THE PAPER

1. The type method; discussion, and statement of criteria used in this paper for choice of types.
2. Alphabetical list of genera, their types, and necessary comments and explanations.
3. Phylogenetic synopsis of the nomenclature including subdivisions of the genera.
4. Acknowledgments.
5. Bibliography.
6. Index to tribes, genera, and their subdivisions.
7. Index to species.

<sup>1</sup> Dates in parentheses refer to the bibliography.

### 1. The Type Method

The type method as incorporated into the International Rules of Botanical Nomenclature, Art. 18 (Briquet 1935) is explained too briefly to serve as a general basis for the choice of types. In order to understand the method, it is necessary to refer to the background of the type method as incorporated into the Rules of 1930. The more important papers dealing with or illustrating the type method are: Arthur et al. (1904: 254-257, 1907: 172-174); Britten et al. (1924); Britton & Brown (1913: ix-x); Brooks (1925: 304-305); Cook (1898, 1900); Green (1925); Hitchcock (1919, 1920, 1921, 1923, 1925: 129-139); Hitchcock & Green (1929: 111-114); Sprague (1926: 96-100); and Underwood (1899: 250-253).

In general the criteria used in selecting types are those recommended by Hitchcock (1919: 333-336). It is well to remember that Article 7. (g): "If it is impossible to select a type under the conditions mentioned above the first of equally eligible species would be chosen." was the last and least criterion recommended, and was not a primary rule. More consideration has been given in the present study to selecting a type which will interpret a genus in its usual sense, provided such choice does not defeat more important considerations, than seems to have been recommended by Hitchcock (1919: 335) in Art. 7. (c). Also, where the choice is available, an additional consideration is weighed before applying Art 7. (g): A species for which there is extant a type specimen is preferred to one for which there is no such historical type plant specimen.

One paramount principle used here in the choice of types is that, if possible, a species assigned to a genus (or other category) by its author should be taken as type. This is not intended to contravene Rule 5 of Sprague (1926: 98), but rather the unwarranted assignment of a species as type which the author of the genus did not place under it and the ignoring of species assigned to a genus by its author, as done, e.g., by Croizat (1937b: 703) for *Tithymalus* Miller, and (1939a: 10) for *Pleuradena* Raf. If the type method is to accomplish its purpose of fixing the application of names, typification must not be altered for mere whims. Consequently, all known typifications of previous authors are accepted in this paper unless actual errors were made in earlier choices.

Sprague's (1926: 96-97) objections to the term "Type-Species" and his consequent substitution of the term "Standard-Species" are not convincing. Sprague, except for his "Rule 5," adopted his rules from Hitchcock (1919: 333-336) and/or earlier publications of the adherents of the American Code of Botanical Nomenclature. The logical propriety of "Rule 5" is very dubious since it proposes to select, in certain cases, as the generic type, a species which its authors did not refer to the genus and which changes the application of the generic name so as to exclude the original species assigned by the author of the genus. Such procedure should call for conservation of the generic name in its altered sense. To allow alteration of the original application of a generic

name merely by one man's choice of a type species leaves too much to the caprice of the individual. There is bound to be endless bickering about cases in which application of a generic name is changed by choosing as type a species not congeneric with those originally included. There is enough trouble about names conserved by allegedly unanimous consent of a committee, or by vote of a botanical congress, without adding to the confusion those conceptual changes made by individuals.

In this study in cases in which the author of a genus never assigned any species as binomials, the first (chronologically speaking) binomial assigned by any author is taken as type as long as it comes within the definition of the genus. If an author originally assigned polynomials to his genus and later binomials, the species chosen as type is that which most clearly is identical with one of the original polynomials.

Avowedly and actually superfluous names are automatically typified and rejected by considering them as merely superfluous renamings of the earliest available name cited in synonymy. This is done regardless of whether there is a diagnosis. A precedent for this action is furnished by the decision that "When on transference to another genus the specific epithet has been applied erroneously in its new position to a different plant, the new combination must be retained for the plant on which the epithet was originally based, and must be attributed to the author who first published it." (Sprague 1936: 76). The discussion of the problem at the last International Botanical Congress gives additional support to my broad interpretation (Sirks 1936:347-354). Unless this principle is recognized, it is a matter of opinion whether a given name is new or merely a substitute. By automatically rejecting and typifying actually and avowedly superfluous names, clarity will be attained. It may be objected that this procedure is unjust and arbitrary.

As far as justice is concerned, there should be no complaint, for the old doctrine of "an eye for an eye and a tooth for a tooth" is no more than justice in nomenclature. If an author knows of an earlier available name he is bound by Articles 16 and 60 (1) (Briquet 1935) to use it. Unless a penalty is provided in a law, obedience to that law is entirely a matter of individual whim. This disposal of avowedly and actually superfluous names thus summarily is arbitrary, but no more so than the action of their authors in proposing them. It is really immaterial whether the above type of name is merely automatically rejected as illegitimate or is rejected and typified with the same entity as the type of the name for which it was substituted, except that, if the application of the substituted name is based on its description rather than the name for which it is substituted, the substitute name might be cited as a synonym of various different names depending on varying interpretations of the description, or might even be maintained as valid. This would cause endless confusion.

It is well to elucidate what is meant by an "avowedly and actually superfluous name." *Pteretis* Raf. was avowedly superfluous since it was substituted

for *Struthiopteris* Willd. on the ground that *Struthiopteris* was "abominable." Nevertheless, since *Struthiopteris* Willd. was preoccupied, *Pteretis*, though avowedly superfluous, was actually a necessary substitution. See Wheeler (1939d: 529) for additional discussion and example.

It may seem inconsistent to accept as validly proposed the genera separated from *Euphorbia* by Haworth (1812: 126-159) who cited *Euphorbia* L. under each new genus as an unqualified synonym, and at the same time reject as invalid the proposal of *Tithymalus* [Tourn.] by DuRoi, Adanson, and Scopoli. The distinction made here is that while Haworth did cite *Euphorbia* L. as a seemingly unqualified synonym of the segregated genera, he nevertheless maintained *Euphorbia* in a restricted sense which included the type, *E. antiquorum*. DuRoi and Scopoli had no members of *Euphorbia sensu strictiore* in their works so their statement of synonymy must be accepted, particularly since Tournefort seems to have applied *Tithymalus* in the sense of *Euphorbia sensu latiore*. Adanson (1765: 611) lists *Euphorbia* L. as a synonym of *Tithymalus*.

## 2. Alphabetical List of Genera and Their Types<sup>1</sup>

ADENOPETALUM Klotzsch & Garcke in Klotzsch (1859: 250); not Turcz., Bull. Soc. Imp. Nat. Moscou 31 (1):416. 1858. Type: *Euphorbia graminea* Jacq.; chosen by Wheeler (1939c: 58) since it is the best known and a widespread member of the group.

ADENORIMA Rafinesque (1838a: 112). Type: *A. punicea* (Swartz) Raf.; based on *Euphorbia punicea* Swartz. This type was designated by Rafinesque, l. c.

AGALOMA Rafinesque (1838a: 116). Type: *Euphorbia corollata* L., assigned by Rafinesque (1840: 95).

AKLEMA Rafinesque (1838a: 114). Type: *A. nudiflora* (Jacq.) Raf.; based on *Euphorbia nudiflora* Jacquin; designated as type by Rafinesque, l. c.

ALECTOROCTONUM Schlechtendal (1847: 252). Type: *A. Scotanum* Schlechtendal. Chosen here because, of the four species assigned to the genus by its author, this is the only one suitable. The two other new species were based on sterile material. The nomenclatorial basis of *A. cotinifolium* is *Euphorbia cotinifolia* by taxonomic inference rather than by definite statement, and, what is worse, Schlechtendal is applying the name to "(specim. ex ins. St. Thomae)." Since the nomenclatorial basis of this name is dubious the name might have to be interpreted on the basis of the specimen of unknown identity from St. Thomas Island. Linnaeus repeatedly stated that *Euphorbia cotinifolia* is native to Curassao.

ALLOBIA Rafinesque (1838a: 116). Type: *A. portlandica* (L.) Raf.; based on *Euphorbia portlandica* L.; the type designated by Rafinesque, l. c.

<sup>1</sup> For final disposition of these genera, see part 6. INDEX, referring them to their phylogenetic position in Part 3.

ANISOPHYLLUM Haworth (1812: 159); not Jack., Select. Stirp. Amer. Hist., 283, T. CLXXX, fig. 5. 1763. Type: *Anisophyllum pepis* (L.) Haw.; based on *Euphorbia Pelis* L.; chosen by Wheeler (1941: 110) since it is a typical and well-known member of the genus.

ANTHACANTHA Lemaire (1855: Misc. 69) as synonym of *Euphorbia* sect. *Anthacanthae*; Lemaire (1857: Misc. 73) in obs. Based on *Euphorbia* sect. *Anthacanthae* Lem.

ANTHOSTEMA Adr. Jussieu (1824a: 56). Type: *A. senegalensis* Jussieu; automatically the type as it was the only species assigned at the time the genus was published.

APLARINA Rafinesque (1838b: 99). Type: *A. prostrata* Raf., chosen by Wheeler (1941: 111) since it was the only species unequivocally assigned to the genus. This was a new species proposed without reference to *Euphorbia prostrata* Aiton. Rafinesque (1840: 97) reduced *Aplarina* to a subgenus of *Xamesike* and transferred (pp. 98-99) both species of *Aplarina* to *Xamesike*. This procedure was taxonomically acceptable. Since, according to Barnhart (1907: 179), *Flora Telluriana*, part 4, where *Xamesike* was published, appeared before *New Flora*, part 4, where *Aplarina* was published, this reduction was nomenclatorially correct.

ARTHROTHAMNUS Klotzsch & Garcke in Garcke (1859: 251). Type: *Arthrothamnus Tirucalli* (L.) Klotzsch & Garcke; based on *Euphorbia Tirucalli* L., first mentioned, and chosen by Millspaugh (1909: 306) probably for that reason. This choice is quite satisfactory.

ATHYMALUS Necker (1790: 353, T. 29, fig. 1). Type: No species were ever assigned to the genus either by its author or anyone else. The identity of this genus seems never to have been elucidated. The reason for this is that Necker's description was scarcely to be interpreted since the terminology employed was rather unique. It is possible, however, to correlate the description with the illustration cited above and satisfactorily demonstrate by the similarity of the explanation of the figure on page 331 with the description of the genus on page 353 that T. 29, fig. 1 illustrated *Athymalus*:

- p. 353. "*Perigynanda propria*, 2-plex."
- p. 331. "*Perigynanda propria*, duplex, triplex simplexve.;"
- p. 353. "*Exterior*, 1-sepala, obconica, cavo-lobata."
- p. 331. "*exterior perigynandae duplicis ordinis*, monosepala, obconica, cavo-lobata fig. 1. a;"
- p. 353. "*Interior*, 5-sepala, cucullato-furcata."
- p. 331. "*interior*, cucullato furcata fig. b.;"

The parallel is sufficiently close to relate convincingly the figure to the description. The figure bears a sufficiently close resemblance to *Euphorbia anacantha* Aiton as illustrated by Sims (1824 t. 2520), to be included at least among the immediate relatives of this species even if it is not conspecific. Thus *Dactylanthus* Haw. is identical with *Athymalus* Necker. *Euphorbia anacantha* Aiton is a typical member of *Dactylanthus* Haw. — See discussion



under *Pedilanthus* of the fact that Necker called his genera "species naturales."

BOJERIA Rafinesque (1837: 95), *nomen provisorium* under *Lacanthis*. Type: *Lacanthis splendens* (Bojer) Raf.; based on *Euphorbia splendens* Bojer ex Hooker.

CALYCOPEPLUS Planchon (1861: 30). Type: *C. ephedroides* Planchon, op. cit., 31; the only species assigned to the genus by its author.

CHAMAESYCE S. F. Gray (1821: 260). Type: *C. maritima* S. F. Gray; automatically the type species since it was the only species assigned to the genus at the time the genus was published. Small (1913: 462) chose this as type. There is an element of truth in Millspaugh's (1909: 300) designation of *Euphorbia Peplis* L. as the type species, for S. F. Gray cited this in synonymy under his *Chamaesyce maritima* which makes this an avowedly (and actually) illegitimate name.

There is a very difficult point as to the ultimate basis of *Chamaesyce maritima*. If possible the species, if any, for which the genus is named, is to be taken as the type species. Therefore *Euphorbia Chamaesyce* L. should be the type species of the genus *Chamaesyce*. The way is not clear for such a choice for S. F. Gray cites both *Euphorbia Peplis* and *E. Chamaesyce* in synonymy under *Chamaesyce maritima*. The emphasis is placed on *Euphorbia Peplis* for that is the plant described, it is maritime, and several names designating the entity *Euphorbia Peplis* appear in synonymy, while *E. Chamaesyce* appears but once. Consequently the type specimen of *Euphorbia Peplis* L., preserved in the Linnaean Herbarium, is also the type specimen of *Chamaesyce maritima* S. F. Gray.

The case of this genus is similar to that of *Tithymalus auct. plur.* but in a lesser degree. It will suffice here to point out that (1) the name *Chamaesyce* is another traditional name and that (2) it was published provisionally as a generic name earlier than 1821.

(1) S. F. Gray attributes his genus to Dioscorides. Wiman (1756: 102) lists *Chamaesyce* among the synonyms of *Euphorbia*.

(2) Rafinesque (1817: 119) published *Chamaesyce* as a subgenus validly and as a genus provisionally in the following words: "They [*Euphorbia supina* Raf., *E. maculata* L., *E. thymifolia* L., *E. littoralis* Raf., & *E. vermiculata* Raf.] all belong to the sub-genus (or perhaps genus!) *Chamaesyce*, which has stipules axillar flowers, and a campanulated four cleft perianthe." There is some doubt as to just what a provisional name is. The original proposal to reject provisional names as not validly published was made by Ramsbottom, Willmott, Sprague, and Wakefield (1929: 16-17 (Art. 44)). In this proposal provisional and eventual names were synonymous. The rule was amended at the 1935 International Botanical Congress (Sirks 1936: 365) in an attempt to distinguish between *nomina provisoria* and *nomina eventualia* or *alternativa*. Provisional names were rejected and eventual or alternative names accepted. Sprague (1936: 75) gives a synopsis of the decision. The distinction attempted

is impossible to make in many cases and it seems best in this case to consider Rafinesque's publication of *Chamaesyce* as a genus as not valid. This decision is somewhat influenced by the writer's (1939d: 528) predilection in favor of rejecting both provisional and eventual names. However, it is true that this case does not fit the only example given of an eventual name. Furthermore, Rules, Art. 16, state that any group can have only one valid name (Briquet 1935).

CHARACIAS S. F. Gray (1821: 259). Type: *Characias purpurea* (Lam.) S. F. Gray, the immediate basis of which was *Tithymalus purpureus* Lam., an avowedly and actually superfluous name based on *Euphorbia characias* L. While it is doubtful whether a name of this sort can ever be validated, the nomenclatorial validity of the name applied to the type species is of little moment here. S. F. Gray may have been trying to avoid a tautonym. The important point is that it is reasonable to assume that the genus *Characias* was named for *Euphorbia characias*, hence the type species of the genus *Characias* should be based on the type of the species *Euphorbia characias*.

CHYLOGALA Fourreau (1869: 150). Type: *Chylogala serrata* (L.) Fourr., based on *Euphorbia serrata* L. This species is automatically the type since it was the only species assigned to the genus at the time it was published.

This genus has been considered a *nomen nudum* by some, perhaps all, authors, e. g., Prokhanov (1933: 57). Nevertheless, Fourreau did refer to "*Euphorbiae carunculares* Boiss. Prodr." which, while a somewhat imperfect and incomplete reference readily leads anyone familiar with the literature of *Euphorbia* to *Euphorbia* section *Tithymalus* § *Carunculares* Boiss., (1862: 111). Thus it is reasonable to consider this genus as validly published under the provisions of the Rules Art. 42 (Briquet, 1935).

CREPIDARIA Haworth (1812:136). Type: *C. myrtifolia* (Miller) Haw.; based on *Tithymalus myrtifolius* Miller; chosen by Wheeler (1939a: 44).

CTENADENA Prokhanov (1933: 28); based on *Euphorbia* sect. *Tithymalus* § *Crotonopsidae* Boiss. Type: *Ctenadena lanata* (Sieb.) Prok.; based on *Euphorbia lanata* Sieb.; automatically the type since it was the only species assigned to either the division by Boissier, l. c., or the genus by Prokhanov.

CUBANTHUS (Boiss.) Millspaugh (1913: 371); based on *Pedilanthus* sect. *Cubanthus* Boissier. Type species: *Cubanthus linearifolius* (Griseb.) Millsp.; based on *Pedilanthus linearifolius* Griseb.; designated by Millspaugh (1913: 372) which choice is satisfactory since Boissier, idem, assigned but this one species to his section.

CYATHAPHORA Rafinesque (1838a: 117). Type: *C. heterophylla* (L.) Raf., based on *Euphorbia heterophylla* L.; chosen here because this was the only clearly stated basis given for the genus. Two other "types" were given first but they were, in the case of the first, a renaming of a probable *sensu* name (the reference given has not been available) and in the case of the second, a name based on two *sensu* names.

CYSTIDOSPERMUM Prokhanov (1933: 25). Type: *C. cheirolepis* (Fischer & Meyer) Prokhanov, based on *Euphorbia cheirolepis* Fischer & Meyer; automatically the type as it was the only species assigned to the genus.

DACTYLANTHES Haworth (1812: 132). Type: *D. anacantha* (Aiton) Haw.; based on *Euphorbia anacantha* Aiton; chosen here because of the three species definitely assigned to the genus this is the best known.

DEMATRA Rafinesque (1840: 96). Type: *D. sericea* Raf.; automatically the type since this was the only species assigned to the genus. The identity of the plant was ascertained by examination of the type (in herb. West Chester State Teachers' College, West Chester, Pennsylvania) which shows that it is *Euphorbia lanata* Sieber. Rafinesque was puzzled by the fruit for he wrote "... fruit very singular, the outer coat is perhaps a calix." The separation of the dehiscent valves into a thin outer layer and a firm inner layer is not unique. Under *Damatra sericea*, Rafinesque makes a statement which is confusing: "Palestina, sent me by Sieber as *E. villosa*, but the previous sp. of Hungary is a *Tithymalis* [sic]." It is possible to guess that by "previous sp. of Hungary" he meant the prior *Euphorbia villosa* Waldst. & Kit. of Hungary; on the other hand, Rafinesque apparently had in his herbarium a specimen collected in Hungary by Dr. Freedly and named *Euphorbia villosa*. That this specimen was probably in Rafinesque's herbarium is suggested by the fact that both Freedly's and Sieber's specimens are now mounted together on the same sheet without indication of which belongs to which original ticket and between is a large "Autikon Botanikon" label. It is easy to relate Sieber's label to his specimen by Rafinesque's description. — *Ctenadena* Prokhanov (1933: 28) is precisely the same concept.

The justification for stating that the specimen at West Chester State Teachers' College is the type is that the specimen is probably from Rafinesque's herbarium, which according to Pennell, *Bartonia* 21:54-55, was bought by Elias Durand. William Darlington, from whom this specimen came, is supposed to have acquired the plants from Durand. Sieber's label reads "Euphorbia villosa Sieber. Palest. E. Durand" which seems to connect Durand satisfactorily with the transaction.

DESMONEMA Rafinesque (1833a: 177). Type: *D. hirta* Raf.; automatically the type since it was the only species assigned to the genus. The identity of this genus is very doubtful. It probably belongs within the limits of *Euphorbia*, *sensu latiore*. Rafinesque seems to have been using some of the obscure terminology of Necker when he described this genus. That Rafinesque was well acquainted with Necker's writings is evident, e. g., Rafinesque (1833c: 19) states "The N. [ew] G. [enera] of Adanson and Necker so long neglected by the Linnaean Botanists, have mostly been lately restored; thus it will be with mine." Later on in this same periodical in "Extra part of No. 6" Rafinesque (1833c) repeats the description of *Desmonema* verbatim. The parallels between the description of Rafinesque and Necker (1790: 331) are:

"perigynanda interior" .....	Necker	} Glands or appendages in different cases.
"Perianth-intern." .....	Rafinesque	
"perigynanda exterior" .....	Necker	} Involucre
"Perianth ext." .....	Rafinesque	

See the more extensive discussion of Necker's terms under *Athymalus*.

No *Euphorbia* answering to Rafinesque's description of *Desmonema hirta* is known to me. The description sounds suspiciously as though it were written from memory. The foliage answers fairly well to that of *Euphorbia dentata* but the cyathia and umbellate inflorescence (inferred from 'invol. triphylo') sound like those of some plant resembling *Euphorbia bicolor* Engelm. & Gray or possibly something like *E. pubentissima* Michaux. Rafinesque (1838a: 113) adds that the plant grows "From Texas to West Kentucky." Until some authentic specimen is found the identity of this genus must remain obscure.

DIADENARIA Klotzsch & Garcke in Klotzsch (1859: 254). Type: *D. Pavnis* Klotzsch & Garcke; chosen by Wheeler (1939a: 44).

DICHOSTEMMA Pierre (1896: 1259). Type: *D. glaucescens* Pierre, l. c. 1260; the only species assigned to the genus at the time it was published.

DICHROPHYLLUM Klotzsch & Garcke in Klotzsch (1859: 249). Type: *Euphorbia marginata* H.B.K.; chosen here as it is a synonym of the independently proposed and earlier *Euphorbia marginata* Pursh which is the best known and widest ranging member of the group. Small (1913: 468) stated that *Dichrophyllum marginatum* (Pursh) Kl. & Gke., the only species included in that particular work of Small's was "typical." Presumably he intended to so designate the type. Bibliographically and nomenclatorially that is an error for Klotzsch & Garcke in Klotzsch (1859) did not mention *Euphorbia marginata* Pursh, but had as the first species *Euphorbia marginata* H.B.K. In 1860 they changed the author to Pursh. Evidently they considered the two taxonomically synonymous as do I.

DICHYLIUM Britton in Britton & Wilson (1924: 499). Type: *Dichyllum Oerstedianum* (K. & G.) Britton; based on *Poinsettia Oerstediana* Klotzsch & Garcke. This species was not only the sole species assigned to the genus but it was "designated as typical." This genus was evidently intended to have the same scope as *Euphorbia* sect. *Dichyllum* Boiss. Britton gave no explanation for the change in spelling.

DIPLOCYATHIUM H. Schmidt (1906: 24). Type species: *D. capitulatum* (Reichb.) H. Schmidt; based on *Euphorbia capitulata* Reichb.; automatically the type as it was the only species assigned to the genus. The genus *Diplocyathium* was not validly published by Schmidt for he did not fulfill the requirements for generic publication given in Rules, Art. 42 and 43 (Briquet 1935). The characterization by Pax (1924: 151) might possibly be considered a validation.

DITRITRA Rafinesque (1838a: 114). Type: *D. hirta* Raf.; chosen since it

was not renamed by Rafinesque as were the other two species included and it was most likely to have been interpreted correctly by Swartz. Three species were described by Rafinesque: *D. obliqua*, *hirta*, and *rotundifolia*; based respectively on *Euphorbia hypericifolia*, *hirta*, and *Chamaesyce*, *sensu* Swartz (1791: 194) *et seq.* It is obvious from Swartz' descriptions that these plants are all members of *Euphorbia* subgenus *Chamaesyce*.

The references given by Swartz such as "S. V. l. c. n. 16" are to Murray (1784). See discussion under *Endoisila* of how it was decided to what work of Swartz Rafinesque referred.

**ELAEOPHORBIA** Stapf (1906a: T. 2823). Type: *Elaeophorbium drupifera* (Thonn.) Stapf; based on *Euphorbia drupifera* Thonn.; automatically the type since it was the only species assigned to the genus. Whether Stapf (1906b: 646) is earlier or later than Stapf (1906a: T. 2823) is not known. The genus appeared as a "new" genus in both works.

**ENDOISILA** Rafinesque (1838a: 114). Type species: "*Endoisila myrsinites* Raf. Euph. do Sw. & c"; automatically the type as only one species was assigned. Rafinesque obviously suffered a *lapsus calami* for Swartz had no such species. Linnaeus did, but *Euphorbia myrsinites* L. is a Mediterranean species. By a process of elimination it is evident that Rafinesque was copying from Swartz (1791), when he described *Endoisila*, *Peccana*, and *Ditritra*. Swartz (1791: 197) has *Euphorbia myrtifolia* L. from which Rafinesque compiled his description of *Endoisila*. (That Linnaeus originally published the species as *myrtillifolia*, and later, probably accidentally, changed it to *myrtifolia* is a side issue of no immediate concern here). It appears that Linnaeus based this species largely on "Brown. jam. 235." Nevertheless there are certain features of the description of *Euphorbia myrtillifolia* which could not have been drawn from P. Browne. Yet Linnaeus had no specimen of this species in his own herbarium until the third edition of the *Species Plantarum*, (1767), according to Jackson (1912: 26). Of course, Linnaeus may have seen a specimen elsewhere. But Swartz excluded "syn. Brown. jam. 235.6." Since Swartz had an original diagnosis and the basis of the Linnaean species is uncertain, the direct and certain method in identifying this genus is to examine Swartz' herbarium (at Stockholm according to De Candolle (1880: 453)) and see what Swartz called "*Euphorbia myrtifolia*." Swartz' plant is probably a member of *Euphorbia* subgenus *Chamaesyce*.

**EPURGA** Fourreau (1869: 150) *nomen nudum*. Type: *Epurga Lathyris* (L.) Fourr.; based on *Euphorbia Lathyris* L., automatically the type since it was the only species assigned.

**ESULA** Haworth (1812: 182). Type: *Esula Dalechampii* Haw.; based on *Euphorbia Esula* L.; chosen here since *Euphorbia Esula* was intended to perpetuate the traditional genus *Esula*. Adr. Jussieu (1819: 396) sets forth this view, and the same author (1824b: 319) definitely mentions that Haworth used the genus. Being, like *Tithymalus*, a traditional name, it is not astonishing to find that the name *Esula* was used, though not properly validated,

prior to 1800. The first post-Linnaean author to employ the name *Esula* was Trew (1754: T. 163). A single species is described under a polynomial. However, Trew was not using *Esula* as a generic name in the usual sense. Beneath the description of "*Esula minor* offic., *Pityusa*." he had "4. NOM. GENER. vid. tab. 123." Then beneath this he had "5. NOM. SPEC." after which he lists many Latin synonyms. It appears that Trew considered his Latin polynomial as a Latin trivial name. Under tab. 123 Trew had "4. NOM. GEN. *Tithymalus*." Under this "*Esula Riv.*" is cited as a synonym. There are two ways of disposing of this name. One is to consider the use of *Esula* by Trew as an irregular use of an apparent generic name as merely the first word of a Latin trivial name. The other is to consider *Esula* Trew as having been published as a synonym of the traditional genus *Tithymalus*. In either event *Esula* was not validly published as a genus.

The second author to use *Esula* in post-Linnaean times was Hill (1755: 349). He did not describe the genus but described two species under it. This, of course, does not constitute valid publication of the genus. Garsault (1767: 169, Pl. 264-265) used the genus, as did Hill, without describing it. (Garsault's plates first appeared in 1764 according to Garsault (1767: iii). See Thellung (1908: 778-793, 901-913) for a discussion of this polynomial work. Wilmott (1935: 90) notes that an explanation of Garsault's plates was published in 1765. A. Eaton (1818: 242) used *Esula* but did not define it. No author is given by Eaton for this genus but no importance is attached to that fact for he omitted authors in his Manual. The vague reference "See Persoon" is given. Persoon (1806: 14) had *Esula* as a defined subdivision of subgeneric rank, of *Euphorbia*. Eaton included in his *Esula* two species which belonged in it and two which did not. Since Eaton did not define his genus and the reference is insufficient and he omitted all authors anyway, it is best to consider his use as another use of the traditional genus *Esula* which was validated by Haworth. S. F. Gray (1821: 257) used *Esula* and credited it to Pliny. Gray's references to specific combination made under the genus by Haworth indicate that he was aware of Haworth's publication. Consequently, since S. F. Gray knew of Haworth's use of *Esula* and also since it was customary to credit traditional genera to their pre-Linnaean authors, there is no reason for considering S. F. Gray's use as a proposal of a new genus.

In the event that Necker's "species naturales" are not to be considered as genera, then it is important to note that, *Keraselma* Necker thus being eliminated, *Galarhoeus* and *Esula* Haw. are the next genera for the concept if *Tithymalus* is not conserved. Hara (1935: 383) reduced *Esula* to synonymy under *Galarhoeus*, thus fixing the usage according to the provision of Rules Art. 56 (Briquet 1935), but *Esula* is preoccupied by the following anyway.

*ESULA* Morandi (1761: 72, Tab. XL). The identity of this genus is obscure since the single polynomial species assigned it is so badly illustrated that I do not recognize it. The best guess is that it is related to *Euphorbia Hermentiana* Lemaire.

*EUMECANTHUS* Klotzsch & Garcke in Klotzsch (1859: 248). Type:



*Euphorbia ariensis* H.B.K., chosen (satisfactorily) by Millspaugh (1916: 412).

EUPHORBIA L. (1753: 450, 1754: 208). Type: *Euphorbia antiquorum* L.; chosen by Millspaugh (1909: 306) and by Hitchcock and Green (1929: 157). According to the Rules, Art 42 (Briquet 1935) the genera used by Linnaeus in *Species Plantarum* are considered as validly published in 1753 even though undefined.

EUPHORBIASTRUM Klotzsch & Garcke in Klotzsch (1859: 252). Type: *Euphorbiastrum Hoffmannianum* Klotzsch & Garcke; chosen here because it was the only species assigned to the genus by its authors. This species remained a *nomen nudum* until Boissier (1862: 99) validated it under *Euphorbia*.

EUPHORBIODENDRON Millspaugh (1909: 305); based on *Euphorbia* Sect. *Tithymalus* § *Laurifoliae* Boiss. Type: *Euphorbia laurifolia* Juss. in Lam.; chosen here. In a way it is unfortunate that this species should be taken as type, for the species is based on a drawing. However, subdivision *Laurifoliae* was obviously named for this species, and it seems rather necessary to choose this species as type for that reason. The genus *Adenorima* Raf. is an earlier generic name for the same concept.

EUPHORBION St.-Lager (1880: 125). This is a mere variant spelling of *Euphorbia*. Saint-Lager proposed to reform botanical nomenclature by changing many terminations of generic and specific names.

EUPHORBIOPSIS Lévillé (1911: 446). Type: *Euphorbiopsis lucidissima* (Lévl. and Vant.) Lévl.; based on *Euphorbia lucidissima* Lévl. and Vant.; automatically the type as it was the original species assigned to the genus. The identity of this genus is uncertain but the disposal of it under *Euphorbia* subg. *Esula* by Pax and Hoffmann (1931: 220) may be correct, however "capsula bacciformis et monococca" can scarcely be reconciled to *Euphorbia*. Handel-Mazzetti (1931: 234) states that it is a member of the gentianaceous genus *Canscora*. However, what he took to be the type "im Edinburgher Herbar" failed to show some of the obvious characters mentioned in the original description of the species. Handel-Mazzetti (1936: 949) cites the specimen he chose as type: "Dapin, Felsen, sehr selten, 1200 m, III. 1910 (Bodmier 2650, Typus: Hb. Edinb.)." Obviously a specimen collected in 1910 could not be the type of a species described in 1906. Besides this anachronism, the type was stated to have been collected by Cavalerie and to be in "herb. Acad. géogr. bot." by which is presumably meant the Académie internationale de Géographie Botanique of Paris. In view of the fact that Handel-Mazzetti took as type a plant which was neither type nor isotype his conclusion as to identity cannot be accepted.

EUPHORBIVM Hill (1755: 136) Type: *Euphorbia antiquorum* L.; chosen here. This choice is justified by the statement of Hill (1756: 158) under his "2. The Euphorbium of the Antients. *Euphorbium antiquorum* . . . Linnaeus calls it *Euphorbia aculeata subrotunda triangularis articulata ramis patenti-*



bus." This phrase name is taken from Linnaeus (1753: 450) under *Euphorbia antiquorum* L. That Hill's "subrotunda" was a merer *lapsus calami* for Linnaeus "subnuda" is evident.

Garsault (1767: 72, Pl. 100) also defined this traditional genus. (See discussion under *Esula* concerning my treatment of later validations of traditional genera and as to date of Garsault's plates). Pl. 100 is plainly a mediocre copy of Pl. 12 from Commelin (1697). The mirror-imaging is due to the failure of the artist who engraved the copy to make a mirror-image on the engraved block. Croizat (1934: 19-30) discusses the identity of this plate with some heat.

GALARHOEUS Haworth (1812: 143). Type: *Galarhoeus Helioscopia* (L.) Haw.; based on *Euphorbia Helioscopia* L.; chosen here. Of the species assigned to this genus by Haworth this is the best known and most wide-spread. There are many variant spellings of this genus. Dalle Torre and Harms (1900: 282) list five including an unintentional variant of their own.

HEXADENIA Klotzsch & Garcke in Klotzsch (1859: 253). Type: *Pedilanthus macrocarpus* Benthham; automatically the type since it was the only species said, at the time of publication, to belong to the genus; accepted by Wheeler (1939a: 45).

KANOPIKON Rafinesque (1838a: 114). Type: *K. atropurpurea* (Broussonet) Raf.; based on *Euphorbia atropurpurea* Broussonet ex Willd.; so indicated by Rafinesque.

KERASELMA Necker (1790: 353, Tab. XXIX, fig. 2). Type: *Euphorbia Esula* L.; chosen here. Necker assigned no species to his genus. The earliest reference I have been able to find (with the assistance of the invaluable Pfeiffer, (1874)) in which *Keraselma* is definitely associated with any species is in Reichenbach (1832: 759) where the name is used as a subdivision of the genus *Euphorbia*. *Esula* Haw. is cited as a synonym and that is correct for the two names apply to the same group. Among the species included in this group by Reichenbach was *Euphorbia Esula* L. Since this is a characteristic member of the group it is chosen as type. Rafinesque (1838a: 116) included *Euphorbia Esula* L. under *Keraselma* subgenus *Esula*.

The above interpretation of *Keraselma* can be justified by the same method used in the case of *Athymalus*. The figure given by Necker is unmistakable. It is only necessary to relate the figure to the description to make the identity clear.

p. 353 "Interior 4-sepala, dentibus adnata, plana, lunato-cornuta, persistens."

p. 331 "alia perignanda exterior, pluridentata fig. 2; interior, 4-sepala, lunato-cornuta a a a."

Adr. Jussieu (1822: 357) and Rafinesque (1838a: 116) both interpreted *Keraselma* Necker in the sense of the figure by which it is identified here.

KOBIOSIS Rafinesque (1840: 94). Type: *K. mellifera* Raf.; based on

"Euph. d[itt]o o[mnes] which, while scarcely a valid way of giving a basynym, is nevertheless obviously intended to mean *Euphorbia mellifera* Aiton as concluded by Pennell (1921:94) .

LACANTHIS Rafinesque (1837: 94). Type: *L. splendens* (Bojer) Raf.; based on *Euphorbia splendens* Bojer; automatically the type since it was the only species assigned.

LATHYRIS Trew (1754: T. 123). This is easily identifiable as *Euphorbia Lathyris* L. from the large well-executed colored plate. No type will be designated since the use of this name, like the use of *Esula* by Trew, *q. v. supra*, is not valid publication of a genus. It may be interpreted as merely the first word of a Latin trivial name and it was definitely cited as a synonym of *Tithymalus* of Ray, Tornefort, etc.

LEPADENA Rafinesque (1838a: 113). Type: *L. leucoloma* (Raf.) Raf.; based on *Euphorbia leucoloma* Raf., an avowedly and actually superfluous name for *Euphorbia marginata* Pursh. See Rafinesque (1838a: 125) where he definitely states that Pursh is the author of the "E. [uphorbia] marginata of some Bot. not of Kunth." which was cited in synonymy under *Euphorbia leucoloma* Rafinesque (1833a: 177).

LEPTOPUS Klotzsch & Garcke in Klotzsch (1859: 249) not Decaisne in Jacquemont, Voy. dans l'Indie 4(Bot.):155, t. 156. 1844.<sup>1</sup> Type: *Euphorbia adiantoides* Lam.; chosen here because, of the two described species said to belong to the genus, this is the only one for which a type specimen may be expected to be extant. According to Jackson (1912) there was never a specimen of *Euphorbia ocymoides* L., the other species, in the Linnaean Herbarium.

LOPHOBIOS Rafinesque (1838a: 116). Type: *Euphorbia terracina* L.; chosen because, of the two species given as examples, this is the only one which fits. The only *Euphorbia cristata* published by 1838 was Heyne ex Roth, Nov. Pl. Spec., 226. 1821, from India which apparently does not come within the scope of the genus as Rafinesque intended it.

LORTIA Rendle (1898: 29). Type: *Lortia erubescens* Rendle; automatically the type as this was the only species included in the genus at the time it was published.

LYCIOPSIS (Boissier) Schweinfurth (1867: 37); based on *Euphorbia* sect. *Lyciopsis* Boiss. Type: *Euphorbia cuneata* Vahl; automatically the type since it was the only species included in either the section or the genus.

MEDUSEA Haworth (1812: 133). Type: Logically it would seem that *Euphorbia caput-medusae* L. should be the type of this genus, but Haworth includes it only as a synonym of his *Medusea major* (Aiton) Haw. through the reference "Mill. dict. ed 8. *Euphorbia* 7" which is *E. caput-medusae* L.

<sup>1</sup> Date according to Sherbron & Woodward, Ann. & Mag. Nat. Hist., ser. 7, 8:334. 1901.

Haworth's citation shows that he believed his plant to be identical with the plant known to Linnaeus in *Hortus Cliffortianus* (the garden, not the book) under a polynomial and named *E. caput-medusae* by Linnaeus in 1753. Berger (1899: 88-92 and 1906: 110) likewise considers *Medusea major* as identical with *Euphorbia caput-medusae* L. Linnaeus included under this name several elements. Berger (1906: 111-113) and N. E. Brown (1915: 329-330) discuss this conglomeration. Conclusion: *Medusea major* (Aiton) Haw. (based on *Euphorbia caput-medusae a major* Aiton) is here chosen as type of *Medusea*. According to Berger and N. E. Brown this is identical with *E. caput-medusae* L. Klotzsch & Garcke in Klotzsch (1859: 251 and 1860: 16) credit this genus to themselves and cite in synonymy *Medusea* Haw. and *Dactylanthus* Haw. According to the Rules, Art. 47 (Briquet 1935) changing the circumscription of a group does not justify changing the author. Reichenbach (1841: 193) used *Medusea* as a numbered subdivision of unstated rank of *Euphorbia* under the variant spelling "4. Medusaea (Haw.) Rchb."

**MONADENIUM** Pax (1894: 126). Type: *M. coccineum* Pax; automatically the type since it was the original species; designated by White, Dwyer, & Sloane (1941: 941).

**MURTEKIAS** Rafinesque (1838a: 116). Type: *M. myrsinites* (L.) Raf.; based on *Euphorbia myrsinites* L., so indicated by Rafinesque.

**NEOGUILLAUMINIA** Croizat (1938b: 398). Type: *Neogillauminia Cleopatra* (Baillon) Croizat; based on *Euphorbia Cleopatra* Baillon; automatically the type since it was the only species referred to the genus.

**NISOMENES** Rafinesque (1838a: 116). Type: "Type *N. diffusa* Raf. Euph. d[itt]o L. auct." Linnaeus published no such species. The only *Euphorbia diffusa* published by 1838 was by Jacquin, Misc. Austr. Bot. Chem. & Hist. Nat. 2:311. 1781. Rafinesque's description: "per.[iantho] lobis 4 lunatis ineq. 2 oppositis duplo major capsula glabra" parallels that part of Jacquin's description of the same parts sufficiently closely to justify the conclusion that Rafinesque was copying Jacquin rather than some other and unknown author: "Petalo quatuor, flava, acute lunata, quorum duo duplo latiora, . . . capsula glabra." While the erroneous basynym given excludes the nomenclatural basing of *Nisomenes diffusa* Raf. on *Euphorbia diffusa* Jacquin, it is still permissible to use taxonomic and bibliographical inference in identifying the two as taxonomically identical. Boissier (1862: 139) identifies *Euphorbia diffusa* Jacq. as a variety of *E. exigua* L.

**PECCANA** Rafinesque (1838a: 114). Type: *P. glauca* Raf.; based on *Euphorbia graminea* L. *sensu* Swartz (1791: 196); automatically the type as it was the only species assigned. The plant described by Swartz sounds like a member of *Euphorbia* subg. *Agaloma*. Again, as in *Endoisila*, Swartz' specimen must be examined.

**PEDILANTHUS** Necker (1790: 354, Tab. XXIX, fig. 4). Type: *P. Tithymaloides* (L.) Poiteau; based on *Euphorbia Tithymaloides* L.; chosen by Millspaugh (1909: 300). This choice is quite satisfactory for this is the

traditional species of this entity. That Tab. XXIX, fig. 4 refers to *Pedilanthus* can be demonstrated by the same method used in the consideration of *Athy-malus*:

p. 354. "Interior, irregularis, 1-sepala, 4-partita, calceiformis, coarctata."

p. 331. "In specie monogamica perigynanda interior, calceiformis, coarctata fig. 4;"

Necker's genera have been challenged by Wilmott in Gilmour (1935: 92) on the ground that Necker called them "species naturales." Authors have exercised a certain amount of license and adopted these "species" as genera when they chose. This course of action is made reasonable by Necker's inclusion of well-known genera such as *Euphorbia* as parallel with his "species naturales." Whether this procedure is justifiable is a moot question. Wilmott in Gilmour (1935: 92) proposed to reject Necker's "Elementa Botanica" along with certain other works. The proposal was referred to a committee which was to report at the International Botanical Congress in 1940 (Sirks 1936). Even though Necker's work is rejected *Pedilanthus* has been proposed for conservation by Bullock (1939) and Wheeler (1939b) and may still be used after it has received the anticipated provisional approval of the Executive Committee in accordance with the provisions of Rule, Art. 22 (Briquet 1935): "When a name proposed for conservation has been provisionally approved by the Executive Committee, botanists are authorised to retain it pending the decision of the next International Botanical Congress." Even though Wilmott's proposal to reject Necker's work is passed at the next Botanical Congress, *Pedilanthus* can be conserved and used. If Necker is excluded then the genus dates from the use of it by Poiteau (1812: 388). These possibilities have been provided for in the proposal for conservation by Wheeler (1939b).

*PETALANDRA* F. Mueller ex Boissier (1862: 27) as the binomial "*Petalandra euphorbioides* F. Mueller" in synonymy under *Euphorbia micradenia* Boissier.

*PETALOMA* Rafinesque ex Baillon (1860: 114) in synonymy under *Euphorbia* section *Petaloma* (*nomen nudum*); Rafinesque ex Boissier (1862: 63) as synonym of *Euphorbia* section *Petaloma* Boiss. Type: *Euphorbia marginata* Pursh; chosen here as type of *Euphorbia* sect. *Petaloma* Boiss. of which the genus *Petaloma* was published as a synonym.

There is an element of comedy in the use of this name. It is quite evident that Boissier did not see Rafinesque's Atlantic Journal. Boissier (1862: 63) cites "Genus *Petaloma* Rafin. Atl. Journ. 177." On this page Rafinesque described *Euphorbia leucoloma* which he finally identified (1838a: 125) as *Euphorbia marginata* Pursh. Rafinesque (1838a: 113) published *Lapadena* which had the same scope as *Euphorbia* section *Petaloma*. Later Rafinesque must have decided that *Petaloma* would be preferable and written Boissier to the effect that such a genus had been published by him in "Atl. Journ. 177." Sometimes Rafinesque failed to distinguish between what he thought of, or wished he had published on a certain date, and what he actually published.

Rafinesque did distribute specimens under the name of *Petaloma leucoloma*, for Baillon (1860: 114) cites this name from Rafinesque's *exsiccatae*.

PLEURADENA Rafinesque (1833b: 182); not *Pleuradenia* Rafinesque, (1825: 2). Type: *Pleuradena coccinea* Raf.; automatically the type as the genus was considered monotypic by Rafinesque. Later Rafinesque (1838a: 113) designated this species as type and noted that *Pleuradena coccinea* was identical with *Poinsettia pulcherrima* (Willd.) R. Graham. Croizat's (1939a: 10) anachronistic typification of *Pleuradena* is invalid for the reasons stated by Wheeler (1939c: 58). The two names *Pleuradena* and *Pleuradenia* are merely orthographic variants of the same name and the first, being later, is excluded by the provisions of the Rules, Art. 70. (Briquet 1935). The jackals of nomenclature will rejoice in the fact that while the specific name *coccinea* is preoccupied under *Euphorbia*, it can be used under *Poinsettia*, and *Pleuradena coccinea* Raf. is prior to *Euphorbia pulcherrima* Willd.

POINSETTIA Graham (1836: 412). Type: *Poinsettia pulcherrima* (Willd.) Graham; based on *Euphorbia pulcherrima* Willd.; automatically the type since it was the only species assigned to the genus at the time of publication. Millspaugh (1909: 304) accepted this as type. For discussion of the typification see Wheeler (1939c: 58-59).

SCLEROCYATHIUM Prokhanov (1933: 30, fig. 7). Type: *Sclerocyathium Popovii* Prokh.; based on *Euphorbia sclerocyathium* E. Kor. & M. Pop.; automatically the type since the genus was considered monotypic by its author.

STENADENIUM Pax (1901: 343). Type: *Stenadenium spinescens* Pax; automatically the type since it was the only species assigned by Pax, l. c.

STERIGMANTHE Klotzsch & Garcke in Klotzsch (1859: 252). Type: *Euphorbia splendens* Bojer; chosen here since, of the two species referred to the genus at the time of publication, this is the earlier and the other, *E. Bojeri* Hooker, is often considered synonymous with *E. splendens*.

SYNADENIUM Boissier (1862: 187). Type: *Synadenium cupulare* (Boiss.) Wh., based on *Euphorbia cupularis* Boiss. which was the basis of the illegitimate *S. arborescens* Boiss. since the apparent basynum of *S. arborescens* was a nomen nudum; designated by White, Dyer, & Sloane (1941: 951).

TIRUCALIA Rafinesque (1838a: 112). No attempt will be made to choose a type for this genus for in describing it Rafinesque was a little more reckless than usual and attempted to ride two horses at once. Such an act is entertaining in both the circus and systematic botany. The genus is obviously named for *Euphorbia Tirucalli* L. (Orthographic exactitude was not numbered among Rafinesque's virtues.) The description seems to be of *Pedilanthus* as far as "per.[iantho] simplex ventricosus" is concerned and Rafinesque states that "This answers to the *Tithymaloides* of Tournefort. . ." But since the genus was named for *Euphorbia Tirucalli* which was said to belong to it and since "lobis planis rotatis" can scarcely be reconciled to *Pedilanthus*, it is best to relegate this genus to the wastebasket of "Genera incertae sedis."

*TITHYMALOIDES* C. Gomez Ortega (1783: 28). (This may have been published earlier by the same author but the rare first edition (1773 fide Pritzel) has not been available). Type: *Tithymaloides myrtifolium* (L.) O. Kuntze; based on *Euphorbia Tithymaloides* L. *myrtifolia* L.; chosen by Wheeler (1939: 45). *Tithymalodes* O. Kuntze (1891: 620) is a mere variant spelling. See discussion by Wheeler, l. c.

*TITHYMALOPSIS* Klotzsch & Garcke in Klotzsch (1859: 249). Type: *Euphorbia corollata* L.; chosen by Small (1913: 469).

*TITHYMALUS*; the traditional genus used by authors other than Miller, Small, Hara, and Croizat. Type: *Euphorbia Peplus* L.; chosen by Millspaugh (1909: 304). This is quite satisfactory as will be shown below. Since authors have generally credited the genus to Adanson (1763) or Scopoli (1772) it will be well to give a chronological history of the pertinent post-Linnaean uses of the genus.

Trew (1754: Tab. 123) validated the genus by reference to several pre-Linnaean works. This use was illegitimate since *Euphorbia* L. was cited in synonymy. — Scopoli (1754: 8) defines the genus in a synoptical key but he has "*Tithymalus* &c." and the context makes it appear that he probably meant more than one genus. — Robbe (1754: 102) assigned polynomials to the genus but did not define it, hence Nieuwland's (1910: 223) suggestion that Robbe's use might have validated the genus may be dismissed. — Duhamel (1755: 339, Pl. 97) described and illustrated the genus but his use is illegitimate since *Euphorbia* L. is cited in synonymy. — Hill (1756: 148) makes the first wholly valid (aside from preoccupation) use of the genus *Tithymalus*. — Adanson (1763: 355, 611) defined the genus but his use is illegitimate since, on page 611 he cites *Euphorbia* L. in synonymy. — Scopoli (1772: 332) defined the genus but his use is illegitimate as he cited *Euphorbia* L. in synonymy. — Adanson and Scopoli are the authors to whom *Tithymalus* [Tourn.] is generally attributed.

Hill's (1756) use of *Tithymalus* is the earliest valid use. Hill (1768) is the first author to assign binomials to the genus. While his binomials can scarcely stand as valid combinations, it is nevertheless evident what he meant taxonomically. Hill (1756 and 1768) understood the genus correctly. It may be protested that Hill made no reference to Tournefort and that *Tithymalus* Adanson which Millspaugh (1909: 304) typified was Tournefort's genus. Tournefort's genus had a broader scope than the customary post-Linnaean usage recognizes, in fact it was roughly equivalent to *Euphorbia* L. However, Millspaugh was entirely at liberty to typify the genus *Tithymalus* as he did.

The use of the traditional *Tithymalus* is very interesting as an example of evolution of a generic concept. As stated above, the pre-Linnaean usage was often, probably prevalingly, in the sense of what is now known as *Euphorbia* L. *sensu latiore*. Yet post-Linnaean usage has been very generally in the sense of all or part of *Euphorbia* sect. *Tithymalus* as defined by Boissier (1862: 99).

The designation by Small (1913: 471) of *Euphorbia dendroides* L. as

type seems superfluous in view of Millspaugh's earlier acceptable typification.

*TITHYMALUS* Miller (1754: *Tithymalus*). Type: *Tithymalus myrtifolius* Miller (1768: *Tithymalus* 1); chosen by Wheeler (1939a: 46). Croizat's (1937b) typification is an obvious anachronism.

Mr. Alain White has found some interesting sidelights on the failure of Millspaugh and Britton to use this genus. Mr. White has sent me excerpts from two letters written in 1915, one by Britton and the other by Millspaugh, filed at New York Botanical Garden, in which the matter of *Tithymalus* Miller versus *Pedilanthus* Necker is discussed. These letters reveal that Britton knew of *Tithymalus* Miller (1754) at the time he was revising the second edition of Britton and Brown, *Illustrated Flora*, which appeared in 1913. Britton refused to accept *Tithymalus* Miller on the ground that under the American Code it was a hyponym. [See Earle (1904: 509) for definition]. Britton even went so far as to say that Miller did not use his *Tithymalus* in subsequent publications. Of course this is an error for Miller used the name in all editions of his *Gardener's Dictionary* which I have examined and in the first binomial edition, the eighth (1768), Miller assigned two binomials to the genus whereupon it ceased to be a hyponym. Only in the ninth and posthumous edition (edited by Thomas Martyn) of the *Gardener's Dictionary* was *Tithymalus* Miller combined with *Euphorbia* L. — Millspaugh's letter indicated a strong predilection for keeping *Pedilanthus*. This is not in the least astonishing in view of the fact that Millspaugh had published a revision of *Pedilanthus* a couple of years earlier in which *Tithymalus* Miller and *T. myrtifolius* Miller and *T. laurocerasifolius* Miller were wholly omitted.

*TORFASADIS* Rafinesque (1838a: 112). Type: *T. canariensis* (L.) Rafin.; based on *Euphorbia canariensis* L., so stated by Rafinesque.

*TREISIA* Haworth (1812: 131). Type: *T. clava* (Jacq.) Haw.; based on *Euphorbia clava* Jacq.; chosen here, because, of the two species, both Jacquin's, included in the genus by Haworth in 1812, this was illustrated by a better plate of Jacquin's than *E. hystrix*. The choice between the two plates is made on the ground that styles, shown in the plate for *Euphorbia clava* Jacq., are of more diagnostic value than staminate flowers, shown in the plate for *Euphorbia hystrix* Jacq. N. E. Brown (1915: 374) objects that the plant described by Haworth could not have been *Euphorbia clava* for he described it as having "petalis pectinato-serratis." Brown believes, reasonably enough, that Haworth always meant glands when he said "petalis" in relation to the Euphorbieae. Perhaps he did, but there seems to have been some confusion, for immediately beneath the diagnosis given by Haworth is quoted another, originally from Aiton (1789: 136) in which the petals are described as "integerrimis." It evidently did not occur to Brown that it was highly probable that Haworth drew his description from the same plants, or their descendants, as those described by Aiton. The most obvious explanation is that Haworth confused the very conspicuous lobes of the involucre, which were pectinate-serrate, with the glands of his other genera. The description is otherwise satisfactory and the basis of the name is clear so there seems to be no reason for renaming



the Hawthornian plant as did Sweet. If *Treisia clava* is confused, *T. hystrix* is confused for the same reason, so *T. clava* is still eligible to be the type.

The operations of Rules, Art. 54 as modified at the last Congress (Sprague 1936: 76) in relation to Art. 18 (Briquet, 1935) have comical possibilities. The apropos portions of Art. 18 are: "The application of names of taxonomic groups is determined by means of *nomenclatural types*. . . . The type . . . of a generic name is a species, . . ." Art. 54, as amended, provides, among other things, that a new combination misapplied, must still be retained for the plant on which the epithet was originally based. Hence it could be argued that if a genus were defined and a single earlier species transferred to it, that, since this species was automatically the type and so fixed the application of the genus, even though the generic description bore no relation to the species included, the generic name would be applied according to the single species comprised. This would be a ridiculous extreme but it is nevertheless possible. But there is no such difficulty here. The generic description is entirely in accordance with characters of the two species included. The only discrepancy is a seeming error in the specific descriptions. The probable explanation for the single error in the specific descriptions is suggested above. While it would seem fatuous to apply a genus as suggested in the extreme hypothetical case given above, it is reasonable to apply the rule in the other direction when the generic diagnosis agrees perfectly with the original diagnosis of the two species included (by transfer) even though there is one seeming error in the non-original specific diagnosis.

TRICHOSTERIGMA Klotzsch & Garcke in Klotzsch (1859: 248). Type: *Euphorbia fulgens* Karwinski; chosen (satisfactorily) by Millspaugh (1917: 4).

TUMALIS Rafinesque (1838a: 114). Type: *T. Bojeri* (Hooker) Raf.; based on *Euphorbia Bojeri* Hooker; so stated by Rafinesque.

VALLARIS Rafinesque (1838: 114), not N. L. Burmann, Fl. Indica, 51. 1768. Type: *Euphorbia Ipecacuanhae* L.; chosen here for the following reasons: While Rafinesque (1838a: 114 and 1840: 96) did not make a sufficiently definite statement of the basis of his name "*V. ipecacuana*" to fully satisfy the requirements for making a new combination, it was nevertheless evident from the context what he meant. Rafinesque either eliminated the rest of the names by reduction to varietal rank, as *portulacoides* and *uniflora*, or the name was a *nomen nudum* as *fimbriata*, or the name was incorrectly applied, as *missurica*. This last calls for an explanation. Rafinesque based his *Euphorbia missurica* solely on a description given by Torrey, Ann. Lyceum N. Y. 2:244. 1827, under the name of *Euphorbia portulacoides* L., on the ground that the description given by Torrey applied to a new species. Rafinesque was right as to its being a new species but otherwise wrong, for the original specimen has been examined and it is a member of subgenus *Chamaesyce* which Rafinesque did not suspect. *E. portulacoides* is at best a variety of *Euphorbia Ipecacuanhae*. Rafinesque obviously had no inkling that

the James specimen really belonged to the subgenus *Chamaesyce* for he included *Euphorbia missurica* with *Euphorbia portulacoides*. Since *Euphorbia missurica* was misunderstood by Rafinesque it would obviously be unsuitable for the type species of this genus.

VENTENATIA Trattinnick (1802: 86). Type: *Ventenatia bracteata* (Jacq.) Tratt.; based on *Euphorbia bracteata* Jacq.; automatically the type since it was the only species assigned; accepted by Wheeler (1939a: 46).

XAMESIKE Rafinesque (1838a: 115). Type: *Xamesike vulgaris* Raf.; based on *Euphorbia Chamaesyce* L.; chosen by Wheeler (1941: 111) because of the two species assigned to the genus at the time it was published this species had a name enough like that of the genus to hint that it suggested the name. The other species was published merely as: "*X. scordifolia serrate lobes*,". This is a rather inadequate diagnosis. Of course it might be inferred that it was based on *Euphorbia scordifolia* but no basynym was given.

There is a question as to whether "*Xamesike*" were a new genus or merely a variant spelling of the traditional "*Chamaesyce*" which was first validated by S. F. Gray. Rafinesque considered it necessary to change *Euphorbia Chamaesyce* to *Xamesike vulgaris* which indicates that he may have considered the change necessary in order to avoid a tautonym. Rafinesque, in publishing *Xamesike*, makes no reference to his earlier use (Rafinesque 1817: 119) of *Chamaesyce*. However, he includes under *Xamesike*, (1840: 97), three species, *X. supina* (Raf.) Raf., *littoralis* (Raf.) Raf., and *vermiculata* (Raf.) Raf. (published earlier by him as *Euphorbia* (1817: 119)): which he stated, *ibid.* belonged "to the sub-genus (or perhaps genus!) *Chamaesyce*,". Consequently *Xamesike* could be treated as merely a variant spelling of *Chamaesyce*. Such muddles are common in Rafinesque's writings.

ZALITEA Rafinesque (1838b: 98). Type: *Zalitea linearis* Raf., the only species assigned to the genus by its author. The description of *Z. linearis* is sufficiently good to convince me that it is conspecific with *Euphorbia hexagona* Nutt., the type species of *Zygophyllidium* Small.

ZYGOPHYLLIDIUM (Boiss.) Small (1903: 714, 1334); based on *Euphorbia* section *Zygophyllidium* Boiss. (by error referred to by Small (1903: 1334) as "subgenus"). Type: *Zygophyllidium hexagonum* (Nutt.) Small; based on *Euphorbia hexagona* Nutt.; assigned by Small (1913: 468). The description of *Zalitea linearis* Raf., the type species of *Zalitea*, is sufficiently lucid to lead to the conclusion that *Zalitea* (1838) is congeneric with *Zygophyllidium* (1903). Nomenclatorial pirates will be interested to know that there are several species which belong to this group.

### 3. Phylogenetic Synopsis of the Nomenclature

After exhausting the resources of the standard nomenclators, systems, and monographs, a search was made through the library of the Gray Herbarium, and many additional subdivisions of genera discovered. It is virtually inevitable

that some names have been overlooked but the following list is far more complete than any found during the search. There has been no attempt made to include in this list all the nomina nuda of unstated rank used to designate groups of species under *Euphorbia*. Many of these, like the following, have been encountered: *Americanae*, *Gerontogaeae*; *Stipulatae*, *Exstipulatae*; *Annuae*, *Perennes*; *Herbaceae*, *Fruticosae*; *Leiospermae*, *Rhytidospermae*. The various uses by various authors of subdivisions of *Euphorbia* are not listed unless they are definitely of different rank than previously proposed for a given name. *Tithymalus* and *Esula* are the best examples of frequently used traditional names. Many German writers, apparently following Koch (1837) used *Tithymalus* and *Esula* to designate subdivisions of *Euphorbia*, frequently without authors and as lettered or numbered subdivisions of unstated rank. Unless definitely proposed in a new rank such names have been omitted in many cases since they would be without force in considerations of priority.

In determining the rank of subdivisional names, only the actual statement of the author of the name has been considered except that under a genus the sign § is interpreted, as is customary, as meaning section, provided it was not used, as was the custom of Boissier (1862) to designate subdivisions of sections. It has been necessary to examine works very carefully to make sure that no statement as to rank has been overlooked. In a few cases unequivocal indication of rank is found in the indices, e. g., Persoon (1806).

In general the order followed in this list is that of Pax & K. Hoffmann (1931). Their arrangement of the subgenera of *Euphorbia* seems to be partially inverted, e. g., subgenus *Chamaesyce* is the most highly evolved in some respects, yet they place it first implying that it is primitive. However, the relationship of these subgenera is reticulate rather than linear and since some are specialized in one direction and some in another, no original arrangement has been attempted here.

The arrangement of names in the following list is according to rank, then chronologically, except that since priority is no consideration if the rank of a name is unknown, names of unknown rank are arranged alphabetically, in their proper place, to facilitate reference.

A. EUPHORBIACEAE [Jaume St. Hilaire (1805: 276, t. 108)] tribe EUPHORBIEAE.<sup>1</sup> Dumortier (1829: 45); type *Euphorbia* L. A. Jussieu (1832:27); Spach (1834: 488, 530); Bartling ex Endlicher (1840: 1108); Klotzsch (1859: 246).

#### TRIBES:

*Euphorbiaceae* tribe *Anthostemeae* Klotzsch (1859: 247); type *Anthostema* A. Juss.

*Euphorbiaceae* tribe *Pedilanthaeae* Klotzsch (1859: 247); type *Pedilanthus* Neck.

*Euphorbiaceae* tribe *Tithymaleae* (Bartl.) Bubani (1897: 90). So far as has been discovered Bartling published no such name.

<sup>1</sup> Pfeiffer (1874: 1301) cited "Euphorbieae Spreng. 1817. Anleit. II. 1. p. 363: ordo Tricoccae." If Sprengel used the name Euphorbieae in the rank of tribe somewhere in his *Anleitung der Gewächse, Zweite Ausgabe, Erster Theil*, 1817, the only effect will be change in author of the tribal name. Casual search failed to locate the name in any rank.

## SUBTRIBES:

*Euphorbiaceae* tribe *Euphorbieae*: The three following are subtribes of *E. t. E.*:

*Anisophyllae* Klotzsch (1859: 247); type *Anisophyllum* Haw.

*Tithymalae* Klotzsch (1859: 247); type *Tithymalus* Scop.

*Neoguillauminiae* Croizat (1938b: 408); type *Neoguillauminia* Croizat.

## SECTION:

*Euphorbiaceae* sect. *Euphorbiaceae* Blume (1825: 631); type *Euphorbia* L. This is not a section in the proper sense but was nevertheless so designated by Blume.

## CATEGORIES OF UNCERTAIN OR UNSTATED RANK:

*Euphorbiaceae*, ? *Euphorbia* Bartling (1830: 372); type *Euphorbia* L. This and other parallel divisions are singular and the rank is unstated.

*Rutaceae* A. *Euphorbieae* Reichenbach (1832: 753); type *Euphorbia* L.

*Rutaceae* A. *Euphorbieae* b. *Tithymaleae* Reichenbach (1832: 755); type *Euphorbia* L.

1. *ANTHOSTEMA* A. Jussieu (1824a: 56, t. 18).

2. *DICHOSTEMMA* PIERRE (1896: 1259).

3. *NEOGUILLAMINIA* Croizat (1938b: 398).

## SECTION:

*Euphorbia* s. *Decadenia* Baillon (1861: 213); type *Euphorbia cleopatra* Baillon.

4. *EUPHORBIA* Linnaeus (1753: 450, & 1754: 208).

## GENUS:

*Euphorbion* Saint-Lager (1880: 125); a mere variant spelling of *Euphorbia* giving what Saint-Lager considered the "correct" Greek termination.

4a. *EUPHORBIA* subgenus *CHAMAESYCE* Raf.

## GENERA:

*Anisophyllum* Haworth (1812: 159).

*Chamaesyce* S. F. Gray (1821: 260); Rafinesque (1817: 119); *nomen provisiorum*.

*Ditritra* Rafinesque (1838a: 114).

*Endoisila* Rafinesque (1838a: 114).

*Xamesike* Rafinesque (1838a: 115)

*Aplarina* Rafinesque (1838b: 99)

*Petalandra* F. Mueller ex Boissier (1862: 27).

## SUBGENERA:

*Euphorbia* sg. *Chamaesyce* Rafinesque (1817: 119); type *Euphorbia supina* Raf., designated by Wheeler (1939c: 51 footnote 2).

*Euphorbia* sg. *Chamaesyce* Caesalp. ex Reichenbach (1841: 193); type *Euphorbia Chamaesyce* L.; designated by Wheeler (1941: 111).

*Euphorbia* sg. *Anisophyllum* (Haw.) Gaucher (1898: 122, & 1902: 294); based on *Anisophyllum* Haw. by information given (1898: 33). Schmidt (1906: 16); Ascherson & Graebner (1898: 469).

*Euphorbia* sg. *Chamaesyce* (S. F. Gray) House (1924: 470); based on *Chamaesyce* S. F. Gray.

*Euphorbia* sg. *Chamaesyce* Jepson (1936: 423 in key); need not necessarily be taken as new but no direct statement of basis given.

*Xamesike* sg. *Aplarina* (Raf.) Rafinesque (1840: 97); based on *Aplarina* Raf.

*Xamesike* sg. *Xamesike* Rafinesque (1840: 97); not defined but presumably based on *Xamesike*.

*Xamesike* sg.? *Xamobala* Rafinesque (1838a: 115); nomen provisorium of uncertain rank and devoid of species; Rafinesque (1840: 97) definitely as subgenus; type *Xamesike supina* (Raf.) Raf., based on *Euphorbia supina* Raf.

#### SECTIONS:

*Euphorbia* s. *Anisophyllum* Roeser (1828: 412); type *Euphorbia Peplis* L., designated by Wheeler (1941: 111). Boissier (1862: 11).

*Euphorbia* s. *Anisophyllum* (Haw.) Webb & Berthelot (1844-50: 236); Baillon (1858b: 284); based on *Anisophyllum* Haw. Fiori in Fiori & Paoletti (1901: 273).

*Euphorbia* s. *Hypericifoliae* Boiss. ex Pojero (1907: 327); based, by implication, on *Euphorbia* sect. *Anisophyllum* Roeser § *Hypericifoliae* Boiss.

*Euphorbia* s. *Nummulariopsis* Boissier (1862: 9, 71); type *Euphorbia peperomioides* Boiss.

*Tithymalus* s. *Anisophyllum* Gomez de la Maza (1897: 152); based on *Euphorbia* sect. *Anisophyllum* Roeser.

*Tithymalus* s. *Anisophyllum* Roeser ex Bubani (1897: 114); nomen nudum; based by implication on *Euphorbia* sect. *Anisophyllum* Roeser.

#### SUBSECTIONS:

*Euphorbia* sect. *Anisophyllum* Roeser: The following are all subsections of *E. s. A.* *Acutae* Boiss. ex Pax (1891: 104); based on *E. s. A.* § *A.* Boiss.

*Chamaesyceae* Boiss. ex Pax (1891: 104); based on *E. s. A.* § *C.* Boiss.

*Cheloneae* Boiss. ex Pax (1891: 105); based on *E. s. A.* § *C.* Boiss.

*Elegantes* Boiss. ex Pax (1891: 104); based on *E. s. A.* § *E.* Boiss.

*Gymnadeniae* Boiss. ex Pax (1891: 105) based on *E. s. A.* § *G.* Boiss.

*Hypericifoliae* Boiss. ex Pax (1891: 104); based on *E. s. A.* § *H.* Boiss.

*Pleidadeniae* Boiss. ex Pax (1891: 105); based on *E. s. A.* § *P.* Boiss.

*Sclerophyllae* Boiss. ex Pax (1891: 105); based on *E. s. A.* § *S.* Boiss.

#### SERIES:

*Euphorbia* s. *Appendiculatae* (Boissier (1862: 11); included all appendiculate sections; "Trib. *Anisophylleae* Kl. et Gke." cited in synonymy, the ultimate basis of which is presumably the genus *Anisophyllum* Haw. This was not a series in the proper sense since it was used as higher in rank than a section.

*Euphorbia* s. *Stipulatae* Boissier (1879: 1082); the stipulate sections including sect. *Anisophyllum* Roeser; a nomen nudum and not a series in the proper sense since it was used as higher in rank than a section.

#### MISCELLANEOUS CATEGORIES:

*Euphorbia* "Tribu" *Anisophyllum* Roeser ex Mutel (1848: 550); based by implication, on *Euphorbia* sect. *Anisophyllum* Roeser.

#### CATEGORIES OF UNSPECIFIED OR UNCERTAIN RANK:

*Chamaesyce*, *Buxifoliae* Small (1933: 792); type *Chamaesyce buxifolia* (Lam.) Small.

*Chamaesyce*, *Cordifoliae* Small (1933: 792); *Chamaesyce cordifolia* (Ell.) Small.

*Chamaesyce*, *Hirtae* Small (1933: 792); type *Chamaesyce hirta* (L.) Millsp.

*Chamaesyce*, *Hyssopifoliae* Small (1933: 792); type *Chamaesyce hyssopifolia* (L.) Small.

*Chamaesyce*, *Maculatae* Small (1933: 792); type *Chamaesyce maculata* (L.) Small in the usual misapplied sense.

- Chamaesyce*, *Polygonifoliae* Small (1933: 792); type *Chamaesyce polygonifolia* (L.) Small.
- Chamaesyce*, *Tracyanae* Small (1933: 792); type *Chamaesyce Tracyi* Small.
- Euphorbia* sect. *Anisophyllum* Roeper § *Acutae* Boissier (1862: 18); type *Euphorbia acuta* Engelm.; designated by Wheeler (1941: 111).
- Euphorbia* sect. *Anisophyllum* Roeper § *Chamaesyceae* Boissier (1862: 27); type *Euphorbia Chamaesyce* L.; designated by Wheeler (1941: 111).
- Euphorbia* sect. *Anisophyllum* Roeper § *Cheloneae* Boissier (1862: 16); type *Euphorbia nummularis* J. D. Hooker.
- Euphorbia* sect. *Anisophyllum* Roeper § *Elegantes* Boissier (1862: 18); type *Euphorbia elegans* Sprengel.
- Euphorbia* sect. *Anisophyllum* Roeper § *Gymnadeniae* Boissier (1862: 11); type *Euphorbia clusiaefolia* H. & A.
- Euphorbia* sect. *Anisophyllum* Roeper § *Hypericifoliae* Boissier (1862: 20); type *Euphorbia hypericifolia* L.; designated by Wheeler (1941: 111).
- Euphorbia* sect. *Anisophyllum* Roeper § *Pleideniae* Boissier (1862: 50); type *Euphorbia Selloi* Klotzsch.
- Euphorbia* sect. *Anisophyllum* Roeper § *Sclerophyllae* Boissier (1862: 12); type *Euphorbia Atoto* Forst.
- Euphorbia* \**Chamaesyceae* Bertoloni (1842: 37); type *Euphorbia Chamaesyce* L.
- Euphorbia* A. *Chamaesyce* Reichenbach (1832: 755); type *Euphorbia Chamaesyce* L.; designated by Wheeler (1941: 111).
- Euphorbia* i. *Chamaesyce* Pers. ex Pfeiffer (1870: 308); nomen nudum, based by implication on *Chamaesyce* Persoon (1806: 12) which was a synonym of a defined but nameless subgenus of *Euphorbia* identical with subg. *Chamaesyce* Raf.
- Euphorbia* \**Dichotomae* Linnaeus (1753: 453); type *Euphorbia Chamaesyce* L.
- Euphorbia* II *Stipulatae* Ledebour (1833: 195); nomen nudum, type *Euphorbia Chamaesyce* L. (in the usual misapplied sense).

#### 4b. EUPHORBIA subgenus AGALOMA (Raf.) House

##### GENERA:

- Agaloma* Rafinesque (1838a: 116).
- Aklema* Rafinesque (1838a: 116).
- Lepadena* Rafinesque (1838a: 113).
- Peccana* Rafinesque (1838a: 114).
- Vallis* Rafinesque (1838a: 114).
- Zalitea* Rafinesque (1838b: 98).
- Alectorocotnum* Schlechtendal (1847: 252).
- Adenopetalum* Klotzsch & Garcke in Klotzsch (1859: 250).
- Dichrophyllum* Klotzsch & Garcke in Klotzsch (1859: 249).
- Eumecanthus* Klotzsch & Garcke in Klotzsch (1859: 248).
- Euphorbiastrum* Klotzsch & Garcke in Klotzsch (1859: 252).
- Leptopus* Klotzsch & Garcke in Klotzsch (1859: 249).
- Tithymalopsis* Klotzsch & Garcke in Klotzsch (1859: 249).
- Trichosterigma* Klotzsch & Garcke in Klotzsch (1859: 248).
- Petaloma* Rafinesque ex Baillon (1860: 114).
- Zygophyllidium* Small (1903: 714, 1334).
- Dichyllum* Britton in Britton & Wilson (1924: 499).

## SUBGENERA:

- Euphorbia* sg. *Zygophyllidium* Boissier ex Small (1903: 1334) as basonym of the genus *Zygophyllidium*, by error since Boissier (1862: 9, 52) used *Zygophyllidium* as a section.
- Euphorbia* sg. *Adenopetalum* Benth. ex Schmidt (1906: 17); based by implication, on sect. *Adenopetalum* Benth. & Hooker; combination not properly made by Schmidt and no definition given. See Wheeler (1939c: 58) for discussion.
- Euphorbia* sg. *Agaloma* (Raf.) House (1924: 471); based on *Agaloma* Raf.
- Euphorbia* sg. *Lepadena* (Raf.) House (1924: 471); based on *Lepadena* Raf.; first reduced to a synonym of *Euphorbia* sg. *Agaloma* by Wheeler (1939c: 57).
- Euphorbia* sg. *Trichosterigma* Jepson (1936: 424 in key); can be traced to the basonym *Trichosterigma* Kl. & Gke. by reference on page 430 to the place where *Euphorbia misera* Benth., the only species of this immediate affinity occurring in California, was erroneously claimed by Jepson to have been transferred to *Trichosterigma*.
- Euphorbia* sg. *Aklema* (Raf.) Croizat (1939a: 13); based on *Aklema* Raf.

## SECTIONS:

- Euphorbia* s. *Alectoroclonum* (Schlecht.) Baillon (1858b: 284); based on *Alectoroclonum* Schlechten. Boissier (1862: 9, 59).
- Euphorbia* s. *Sparsiflorae* Engelm. (1859: 193); nomen nudum; type *Euphorbia misera* Benth.
- Euphorbia* s. *Zygophylleae* Engelm. (1859: 190); nomen nudum; type *Euphorbia hexagona* Nutt.
- Euphorbia* s. *Crossadenia* Boissier (1862: 9, 64); type *Euphorbia sarcodes* Boiss.
- Euphorbia* s. *Cyttarospermum* Boissier (1862: 9, 53); type *Euphorbia graminea* Jacq.
- Euphorbia* s. *Dichilium* Boissier (1862: 9, 58); type *Poinsettia Oerstediana* Kl. & Gke., "designated as typical" of the genus *Dichilium*, which is based by implication on sect. *Dichilium*, by Britton in Britton & Wilson (1924: 499).
- Euphorbia* s. *Ephedropeplus* Mueller (1874: 668); type *Euphorbia gymnoclada* Boiss.
- Euphorbia* s. *Euphorbiastrum* (Kl. & Gke.) Boissier (1862: 10, 98); based on *Euphorbiastrum* Kl. & Gke.
- Euphorbia* s. *Petaloma* Boissier (1862: 9, 63); type *Euphorbia marginata* Pursh.
- Euphorbia* s. *Portulacastrum* Boissier (1862: 9, 69); type *Euphorbia Pentlandi* Boiss.
- Euphorbia* s. *Stachydium* Boissier (1862: 9, 65); type *Euphorbia comosa* Vell.
- Euphorbia* s. *Tithymalopsis* (Kl. & Gke.) Boissier (1862: 9, 66); based on *Tithymalopsis* Kl. & Gke.
- Euphorbia* s. *Trichosterigma* [as *Tricherostigma*] (Kl. & Gke.) Boissier (1862: 9, 68); based on *Trichosterigma* Kl. & Gke.
- Euphorbia* s. *Zygophyllidium* Boissier (1862: 9, 52); type *Euphorbia hexagona* Nutt., assigned by Small (1913: 468) as type of genus *Zygophyllidium* (as *Z. hexagonum*).
- Euphorbia* s. *Adenopetalum* (Kl. & Gke.) Benth. & Hooker (1880: 258); based on *Adenopetalum* Kl. & Gke.
- Euphorbia* s. *Ephedromorpha* Bartlett (1911: 343); type *Euphorbia ephedromorpha* Bartlett.

## SUBSECTIONS:

- Euphorbia* sect. *Adenopetalum* (Kl. & Gke.) Benth. & Hooker. The first eleven of the following are subsections of *E. s. A.*
- Alectoroclonum* (Schlecht.) Pax (1891: 106); based on *Alectoroclonum* Schlechten.
- Crossadenia* Boiss. ex Pax (1891: 106); based on *Euphorbia s. C.* Boiss.
- Cyttarospermum* Boiss. ex Pax (1911: 106); based on *Euphorbia s. C.* Boiss.



- Dichilium* Boiss. ex Pax (1891: 106); based on *Euphorbia* s. *D.* Boiss.  
*Ephedropeplus* Muell. Arg. ex Pax (1891: 106); based on *Euphorbia* s. *E.* Muell. Arg.  
*Petaloma* Raf. ex Pax (1891: 106); defined; type *Euphorbia marginata* Pursh.  
*Portulacastrum* Boiss. ex Pax (1891: 106); based on *Euphorbia* s. *P.* Boiss.  
*Stachydium* Boiss. ex Pax (1891: 106); based on *Euphorbia* s. *S.* Boiss.  
*Tithymalopsis* Kl. & Gke. ex Pax (1891: 106); based on *Tithymalopsis* Kl. & Gke.  
*Trichosterigma* [as *Tricherostigma*] Kl. & Gke. ex Pax (1891: 106); based on *Trichosterigma* Kl. and Gke.  
*Zygophyllidium* Boiss. ex Pax (1891: 106); based on *Euphorbia* s. *Z.* Boiss.  
*Euphorbia* sect. *Tithymalus* s. *Ipecacuanhae* Boiss. ex Pax (1891: 109); based on *E.* s. *T.* § *I.* Boiss.  
*Euphorbia* subgenus *Agaloma* (Raf.) House sect. *Cytarospermum* Boiss. s. *Leptopus* (Kl. & Gke.) Wheeler (1939e: 44); based on *Leptopus* Kl. & Gke.

## CATEGORIES OF UNSPECIFIED OR UNCERTAIN RANK:

- Euphorbia* *E. Petaloma* Raf. ex Baillon (1860: 114); nomen nudum; type *Euphorbia leucoloma* Raf.  
*Euphorbia* sect. *Stachydium* § *Americanae* Boissier (1862: 65); type *Euphorbia comosa* Vell.  
*Euphorbia* sect. *Tithymalus* § *Ipecacuanhae* Boissier (1862: 101); type *Euphorbia Ipecacuanhae* L.  
*Euphorbia* *F. Trichosterigma* (Kl. & Gke.) Baillon (1860: 114); based on *Trichosterigma* Kl. & Gke.

## 4c. EUPHORBIA subgenus POINSETTIA (Grah.) House.

## GENERA:

- Pleuradena* Rafinesque (1833: 182).  
*Poinsettia* Graham (1836: 412)  
*Cyathophora* Rafinesque (1838a: 117).

## SUBGENERA:

- Euphorbia* sg. *Pleuradena* Rafinesque (1833: 182); nomen provisorium for the genus *Pleuradena*.  
*Euphorbia* sg. *Poinsettia* (Grah.) House (1924: 472); based on *Poinsettia* Grah. Jepson (1936: 424 in key).  
*Euphorbia* sg. *Pleuradena* (Raf.) Croizat (1939a: 10); based on *Pleuradena* Raf.

## SECTIONS:

- Euphorbia* s. *Poinsettia* (Grah.) Baillon (1858b: 284); based on *Poinsettia* Grah. Boissier (1862: 10, 71).  
*Euphorbia* s. *Cyathophorae* Engelm. (1859: 190); nomen nudum; included various species of subg. *Poinsettia* including *E. cyathophora* Murr. as a synonym of *E. heterophylla* L.

## SUBSECTION:

- Euphorbia* subg. *Aglema* (Raf.) Croizat sect. *Dichilium* Boiss. s. *Stormiæ* Croizat (1939a: 13, 14 as "*Stormiæ*"); type *Euphorbia Stormiæ* Croizat which is closely related to if not conspecific with *E. radians* Benth.

## CATEGORIES OF UNSPECIFIED OR UNCERTAIN RANK:

- Euphorbia* *K. Pleuradena* (Raf.) Baillon (1860: 116); based on *Pleuradena* Raf.  
*Tithymalus* \**Annui* Haworth (1812: 141); type *Tithymalus heterophyllus* (L.) Haw. based on *Euphorbia heterophylla* L.

*Euphorbia* ? *Eupleuradena* Croizat (1939a: 11); based, by implication, on *Euphorbia* subg. *Pleuradena* (Raf.) Croizat.

4d. EUPHORBIA subgenus EREMOPHYTON (Boiss.)

GENUS:

*Cystidospermum* Prokhanov (1933: 25).

SUBGENUS:

*Euphorbia* sg. **Eremophyton** (Boiss.) comb. nov.; based on *Euphorbia* sect. *Eremophyton* Boiss.

SECTIONS:

*Euphorbia* s. *Cheirolepidium* Boissier (1862: 9, 70); type *Euphorbia cheirolepis* F. & M. First reduced to synonymy under sect. *Eremophyton* by Benthams & Hooker (1880: 260).

*Euphorbia* s. *Eremophyton* Boissier (1862: 9, 70); type *Euphorbia eremophila* A. Cunningham.

*Euphorbia* s. *Pseudacalypha* Boissier (1862: 10, 98); type *Euphorbia acalyphoides* Hochst. First reduced to synonymy under sect. *Eremophyton* by Benthams & Hooker (1880: 260).

*Euphorbia* s. *Eremophila* Benthams & F. Mueller (1873: 45); type *Euphorbia eremophila* A. Cunningham.

*Euphorbia* s. *Bongium* Boiss. ex Benthams & Hooker (1880: 260); as synonym of sect. *Eremophyton*. Presumably published earlier elsewhere.

*Euphorbia* s. *Holstianae* Pax & K. Hoffmann (1921: 148) type *Euphorbia pseudoholstii* Pax.

SUBSECTIONS:

*Euphorbia* sect. *Eremophyton* Boiss.: The following are all subsections of *E. s. E. Eueremophyton* Pax (1891: 107); based on *Euphorbia* sect. *Eremophyton* Boiss.

*Pseudacalypha* Boiss. ex Pax (1891: 107); defined; based by implication on *Euphorbia* sect. *Pseudacalypha* Boiss.

*Cheirolepidium* Boiss. ex Pax & K. Hoffman (1931: 213); based on *Euphorbia* sect. *Cheirolepidium* Boiss.

*Holstianae* (Pax & K. Hoffm.) Pax & K. Hoffmann (1931: 213); based on *Euphorbia* sect. *Holstianae* Pax & K. Hoffm.

4e. EUPHORBIA subgenus LYCIOPSIS (Boiss.)

GENUS:

*Lyciopsis* (Boiss.) Schweinfurth (1867: 37).

SUBGENUS:

*Euphorbia* subgenus **Lyciopsis** (Boiss.) comb. nov.; based on *Euphorbia* sect. *Lyciopsis* Boiss.

SECTIONS:

*Euphorbia* s. *Lyciopsis* Boissier (1862: 10, 97); type *Euphorbia cuneata* Vahl.

*Euphorbia* s. *Espinosa* Pax & K. Hoffmann in Pax (1921: 149); type *Euphorbia espinosa* Pax.

*Euphorbia* s. *Lignosa* Pax & K. Hoffmann in Pax (1921: 150); type *Euphorbia lignosa* Marl.

SUBSECTIONS:

*Euphorbia* sect. *Lyciopsis* Boiss.: The following are all subsections of *E. s. L.*

*Epinosae* (Pax & K. Hoffm.) Pax & K. Hoffmann (1931: 213); based on *Euphorbia* sect. *Epinosae* Pax & K. Hoffm.

*Eulyciopsis* Pax & K. Hoffmann (1931: 213); based on *Euphorbia* sect. *Lyciopsis* Boiss.

*Lignosae* (Pax & K. Hoffm.) Pax & K. Hoffmann (1931: 213); based on *Euphorbia* sect. *Lignosae* Pax & K. Hoffm.

#### 4f. EUPHORBIA subgenus TITHYMALUS Pers.

##### GENERA:

*Euphorbium* Hill (1755: 136).

*Esula* Morandi (1761: 72, T. XL).

*Athymalus* Necker (1790: 353, T. 29, fig. 1).

*Dactylanthus* Haworth (1812: 132).

*Medusea* Haworth (1812: 133).

*Treisia* Haworth (1812: 131).

*Bojeria* Rafinesque (1837: 95).

*Lacanthia* Rafinesque (1837: 94).

*Tirucalia* Rafinesque (1838a: 112) in part.

*Torfasadis* Rafinesque (1838a: 112).

*Tumalis* Rafinesque (1838a: 114).

*Anthacantha* Lemaire (1855: Misc. 69).

*Arthrothamnus* Klotzsch & Garcke in Klotzsch (1859: 251).

*Sterigmanthe* Klotzsch & Garcke in Klotzsch (1859: 252.)

##### SUBGENERA:

*Euphorbia* sg. *Tithymalus* Persoon (1806: 10); type *Euphorbia antiquorum* L. Proposed without reference to earlier uses of *Tithymalus*.

*Euphorbia* sg. *Athymalus* Necker ex Reichenbach (1828: 194); nomen nudum, based by implication on *Athymalus* Necker.

*Euphorbia* sg. *Euphorbia* Necker ex Reichenbach (1828: 194); nomen nudum, based by implication on *Euphorbia* as limited by Necker.

*Dactylanthus* sg. *Anacantha* Rafinesque (1838a: 112); provisional; nomen nudum. No species assigned but named for *Dactylanthus anacantha* (Ait.) Haw., based on *Euphorbia anacantha* Aiton.

*Dactylanthus* sg. *Medusita* Rafinesque (1838a: 112); provisional. No species assigned but apparently named for "*E.[uphorbia] medusa*" (*E. medusae* Thunb. or *E. caput medusae* L. ?).

*Euphorbia* sg. *Alskebra* Rafinesque (1838a: 112); defined as the smooth species of the fleshy leafless spinose species. No species assigned to this subgenus.

*Euphorbia* sg. *Sadida* Rafinesque (1838a: 112); defined as the spinose species of the fleshy leafless spinose species: No species assigned to this subgenus.

*Euphorbia* sg. *Dactylanthus* Haw. ex Reichenbach (1841: 193); nomen nudum, based by implication on *Dactylanthus* Haw.

*Euphorbia* sg. *Euphorbia* L. ex Reichenbach (1841: 193); nomen nudum, based by implication on *Euphorbia* in a restricted sense.

*Euphorbia* sg. *Medusaea* Haw. ex Reichenbach (1841: 193); nomen nudum, based by implication on *Medusea* Haw.

*Euphorbia* sg. *Treisia* Haw. ex Reichenbach (1841: 193); nomen nudum, based by implication on *Treisia* Haw.

##### SECTIONS:

*Euphorbia* s. *Aculeatae* Haworth (1827: 275); type *Euphorbia caerulea* Haw.

- Euphorbia* s. *Aphyllis* Webb & Berthelot (1844-50: 253); type *Euphorbia aphylla* Brouss.
- Euphorbia* s. *Cereis* Webb & Berthelot (1844-50: 255); type *Euphorbia canariensis* L.
- Euphorbia* s. *Aculeatae* Lemaire (1855: Misc. 68); type *Euphorbia caerulescens* Haw.
- Euphorbia* s. *Anthacanthae* Lemaire (1855: Misc. 69); type *Euphorbia heptagona* L.
- Euphorbia* s. *Medusea* [as *Medusaea*] Haw. ex Baillon (1858: 284); based on *Medusea* Haw. Pax (1921: 161).
- Euphorbia* s. *Treisia* Haw. ex Baillon (1858: 284); based on *Treisia* Haw. Berger (1906: 11, 119); Pax (1921: 163).
- Euphorbia* s. *Arthrothamnus* (Kl. & Gke.) Boissier (1862: 10, 74); based on *Arthrothamnus* Kl. & Gke.
- Euphorbia* s. *Diacanthium* Boissier (1862: 10, 78); type *Euphorbia splendens* Bojer.
- Euphorbia* s. *Euphorbium* Boissier (1862: 10, 85); type *Euphorbia anacantha* Ait.
- Euphorbia* s. *Goniostema* Baillon ex Boissier (1862: 10, 77); type *Euphorbia lophogona* Lam.
- Euphorbia* s. *Tirucalli* Boissier (1862: 10, 94); type *Euphorbia Tirucalli* L.
- Tithymalus* s. *Diacanthium* (Boiss.) Gómez de la Maza (1897: 152); based on *Euphorbia* s. *Diacanthium* Boiss.
- Euphorbia* s. *Ligularia* O. Kuntze in Post & Kuntze (1904: 223); name taken from Rumpf, which, according to Croizat (1939b: 295) is probably *Euphorbia edulis* Lour.
- Euphorbia* s. *Anthacantha* (Lem.) Berger (1906: 10, 88); based on *Anthacantha* Lem. Pax (1921: 160).
- Euphorbia* s. *Dactylanthus* Haw. ex Berger (1906: 10, 104); based on *Dactylanthus* Haw. Pax (1921: 161).
- Euphorbia* s. *Meleuphorbia* Berger (1906: 10, 101); type *Euphorbia meloformis* Ait., designated by Pax (1921: 161).
- Euphorbia* s. *Pteroneurae* Berger (1906: 28); type *Euphorbia pteroneura* Berger.
- Euphorbia* s. *Pseudeuphorbium* (Pax) Berger (1906: 11, 115), Pax (1921: 163); based on *Euphorbia* s. *Eremophylon* Boiss. subsect. *Pseudeuphorbium* Pax.
- Euphorbia* s. *Pseudomedusea* Berger ex Pax (1921: 163); type *Euphorbia esculenta* Marl.
- Euphorbia* s. *Tekeanae* Croizat (1938a: 119); type *Euphorbia teke* Schweinf. designated by Croizat l. c. Spelling changed to *Tekeanae* by Croizat (1939b: 295).

## SUBSECTIONS:

- Euphorbia* sect. *Aculeatae* Haw. s. *Florispinae* Haworth (1827: 275); type *Euphorbia stellaespina* Haw.
- Euphorbia* sect. *Aculeatae* s. *Sterilispinae* Haworth (1827: 275); type *Euphorbia caerulescens* Haw.
- Euphorbia* sect. *Euphorbium* Boiss.: The next four are subsections of *E. s. E.*
- Diacanthium* (Boiss.) Benth & Hooker (1880: 26); based on *Euphorbia* sect. *Diacanthium* Boiss. This is the first reduction of one of these two simultaneously published sections to a subordinate category under the other.
- Goniostema* (Baill.) Benth & Hooker (1880: 260); based on *Euphorbia* sect. *G. Baillon* by the vague reference on page 259 lines 6 and 7. Pax & K. Hoffmann (1931: 214).
- Tirucalli* (Boiss.) Benth & Hooker (1880: 260); based on *Euphorbia* sect. *T. Boiss.*
- Treisia* (Haw.) Benth & Hooker (1880: 260); based on *Treisia* Haw.
- Euphorbia* sect. *Eremophylon* s. *Pseudeuphorbium* Pax (1891: 107); type *Euphorbia Marlothii* Pax, a later synonym of *E. Monteiri* Hook. f. Judging by the related

species illustrated by White, Dyer, & Sloane (1941) this species is readily included in subg. *Tithymalus* Pers.

*Euphorbia* sect. *Diacanthium* Boiss.: The next four are subsections of *E. s. D.*

*Diacanthae* Pax (1921: 155); based by implication on *Euphorbia* sect. *Diacanthium* § *Diacanthae* Pax.

*Scolopendriae* Berger ex Pax (1921: 160); based by implication on *Euphorbia* sect. *Diacanthium* "Gruppe" *Scolopendriae* Berger.

*Tetracanthae* Pax (1921: 159); based by implication on *Euphorbia* sect. *Diacanthium* § *Tetracanthae* Pax.

*Triacanthae* Pax (1921: 159); based by implication on *Euphorbia* sect. *Diacanthium* § *Triacanthae* Pax.

*Euphorbia* sect. *Euphorbium* Boiss.: The next seven are subsections of *E. s. E.*

*Anthacantha* (Lem.) Pax & K. Hoffmann (1931: 216); based on *Anthacantha* Lem.

*Arthrothamnus* (Kl. & Gke.) Pax & K. Hoffmann (1931: 213); based on genus *Arthrothamnus* Kl. & Gke.

*Dactylanthus* (Haw.) Pax & K. Hoffmann (1931: 216); based on *Dactylanthus* Haw.

*Medusea* (Haw.) Pax & K. Hoffmann (1931: 216); based on *Medusea* Haw.

*Meleuphorbia* (Berger) Pax & K. Hoffmann (1931: 216); based on *Euphorbia* sect. *Meleuphorbia* Berger.

*Pseudomedusea* (Berger) Pax & K. Hoffmann (1931: 216); based on *Euphorbia* sect. *Pseudomedusea* Berger.

*Pteroncurae* (Berger) Pax & K. Hoffmann (1931: 214); based on *Euphorbia* sect. *Pteroncurae* Berger.

*Euphorbia* subg. *Tithymalus* Pers. subsect. *Euneriifoliae* [as *Eunefoliae*, corrected by Croizat in litt., Oct. 7, 1942] Croizat (1939a: 295); type not designated by Croizat but presumably intended to have been *Euphorbia neriifolia* L. though *E. edulis* Lour. was the only species included!

*Euphorbia* subg. *Tithymalus* subsect. *Sudaniceae* [sic] Croizat (1939a: 295); nomen nudum; type *Euphorbia sudanica* Chev., designated by Croizat, l. c.

#### MISCELLANEOUS CATEGORIES:

*Euphorbia* [tribu] *Euphorbium* Isnard ex Duchartre (1857: 42); type *Euphorbia antiquorum* L.

*Euphorbia* sect. *Diacanthium* Boiss.: The five following were each termed "Gruppe" under *E. s. D.*

*Compressae* Berger (1906: 30, 40); type *Euphorbia Nyikae* Pax.

*Polygonae* Berger (1906: 30, 53); type *Euphorbia tetragona* Haw. (*E. polygona* Haw. was not included in this group).

*Scolopendriae* Berger (1906: 30, 38); type *Euphorbia uncinata* DC., chosen since named for *E. scolopendria* Donn which was given by Berger as a synonym of *E. uncinata*.

*Splendentes* Berger (1906: 30); type *Euphorbia splendens* Bojer.

*Trigonae* Berger (1906: 30, 43); type *Euphorbia trigona* Haw.

#### CATEGORIES OF UNCERTAIN OR UNSPECIFIED RANK:

*Euphorbia* sect. *Anthacanthae* Lem. a. *Cereoides* Lemaire (1855: Misc. 69); nomen nudum, type *Euphorbia heptagona* L.

*Euphorbia* sect. *Anthacanthae* Lem. b. *Echinocactoides* Lemaire (1855: Misc. 69); nomen nudum; type *Euphorbia meloformis* Ait.

- Euphorbia* k. *Aphyllis* Webb ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Euphorbia* sect. *Aphyllis* Webb & Berthelot.
- Euphorbia* C. *Arthrothamnus* Kl. & Gke. ex Baillon (1860: 106); based on *Arthrothamnus* Kl. & Gke.
- Euphorbia* m. *Cereis* Webb ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Euphorbia* sect. *Cereis* Webb & Berthelot.
- Euphorbia* B. *Cereopsis* Baillon (1860: 104); nomen nudum; type *Euphorbia officinarum* L.
- Euphorbia* c. *Dactylanthes* Haw. ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Dactylanthes* Haw.
- Euphorbia* sect. *Diacanthium* Boiss.: The following seven are subdivisions of *E. s. D.*:  
 §*Biaculeatae* Boissier (1862: 79); nomen nudum; type *Euphorbia splendens* Bojer.  
 §*Diacanthae* Pax (1904: 63-64); type *Euphorbia splendens* Bojer.  
 §*Intermediae* Pax (1904: 63, 84); type *Euphorbia breviarticulata* Pax.  
 §*Monacanthae* Pax (1904: 63); type *Euphorbia monacantha* Pax.  
 §*Tetracanthae* Pax (1904: 63, 80); type *Euphorbia tetracantha* Pax.  
 §*Triacanthae* Pax (1904: 63, 77); named for *Euphorbia triacantha* Ehrenb., but *Euphorbia* sect. *Diacanthium* §*Triaculeatae* Boiss. based on *Euphorbia triaculeata* Forsk. cited in synonymy.  
 §*Triaculeatae* Boissier (1862: 85); type *Euphorbia triaculeata* Forsk.
- Euphorbia* a. *Euphorbia* Haw. ex Pfeiffer (1870: 308); nomen nudum, based by implication on *Euphorbia* as restricted by Haw.
- Euphorbia* sect. *Euphorbium* subsect. *Diacanthium* (Boiss.) Benth. & Hook.: The following seven are subdivisions of *E. s. E. s. D.*:  
 §*Compressae* (Berger) Pax & K. Hoffmann (1931: 215); based on *Euphorbia* sect. *Diacanthium* "Gruppe" *Compressae* Berger.  
 §*Polygonae* (Berger) Pax & K. Hoffmann (1931: 216); based on *Euphorbia* sect. *Diacanthium* "Gruppe" *Polygonae* Berger.  
 §*Scolopendriae* (Berger) Pax & K. Hoffmann (1931: 215); based on *Euphorbia* sect. *Diacanthium* "Gruppe" *Scolopendriae* Berger.  
 §*Splendentes* (Berger) Pax & K. Hoffmann (1931: 214); based on *Euphorbia* sect. *Diacanthium* "Gruppe" *Splendentes* Berger.  
 §*Tetracanthae* (Pax) Pax & K. Hoffmann (1931: 216); based on *Euphorbia* sect. *Diacanthium* §*Tetracanthae* Pax.  
 §*Triacanthae* (Pax) Pax & K. Hoffmann (1931: 216); based on *Euphorbia* sect. *Diacanthium* §*Triacanthae* Pax.  
 §*Trigoniae* (Berger) Pax & K. Hoffmann (1931: 215); based on *Euphorbia* sect. *Diacanthium* "Gruppe" *Trigoniae* Berger.
- Euphorbia* H. *Coniostema* Baillon (1860: 114); nomen nudum, type *Euphorbia lophogona* Lam.
- Euphorbia* d. *Medusea* Haw ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Medusea* Haw.
- Euphorbia* G. *Sterigmanthe* Kl. & Gke. ex Baillon (1860: 114); based by implication on *Sterigmanthe* Kl. & Gke.
- Euphorbia* †*Succulentae* ††*Cereastrae* Lemaire (1855: Misc. 68); nomen nudum including sections *Aculeatae* and *Anthacanthae* Lem.
- Euphorbiae* e. *Tithymalus* Pers. ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Euphorbia* subg. *Tithymalus* Pers.
- Euphorbia* b. *Treisia* Haw. ex Pfeiffer (1870: 308); nomen nudum, based by implication on *Treisia* Haw.

*Tithymalus* \**Graciles* Haworth (1812: 138); type *Tithymalus tirucalli* based on *Euphorbia tirucalli* L.

4g. EUPHORBIA subgenus RHIZANTHIUM (Boiss.)

SUBGENUS:

*Euphorbia* sg. **Rhizanthium** (Boiss.) comb. nov., based on *Euphorbia* sect. *Rhizanthium* Boiss.

SECTIONS:

*Euphorbia* s. *Caulanthium* Boissier (1862: 10, 76); type *Euphorbia sessiliflora* Roxb.  
*Euphorbia* s. *Rhizanthium* Boissier (1862: 10, 92); type *Euphorbia tuberosa* L.

SUBSECTIONS:

*Euphorbia* sect. *Euphorbium* Boiss. s. *Rhizanthium* (Boiss.) Denis (1921: 41, 66); based on *Euphorbia* sect. *Rhizanthium* Boiss.

4h. EUPHORBIA subgenus ESULA Pers.

GENERA:

*Lathyrus* Trew (1754: T. 123).

*Tithymalus* Trew (1754: T. 123); Duhamel (1755: 339, Pl. 97); Hill (1756: 148);

Adanson (1763: 355, 611); Scopoli (1772: 332).

*Keraselma* Necker (1790: 353, T. XXIX, fig. 2).

*Esula* Haworth (1812: 182).

*Galarhoeus* Haworth (1812: 143).

*Characias* S. F. Gray (1821: 259).

*Adenorima* Rafinesque (1838a: 112).

*Allobia* Rafinesque (1838a: 116).

*Kanopiķon* Rafinesque (1838a: 114).

*Lophobios* Rafinesque (1838a: 116).

*Murtekias* Rafinesque (1838a: 116).

*Nisomenes* Rafinesque (1838a: 116).

*Dematra* Rafinesque (1840: 96).

*Kobiosis* Rafinesque (1840: 94).

*Chylogala* Fourreau (1869: 150).

*Epurga* Fourreau (1869: 150).

*Diplocyathium* Schmidt (1906: 24).

*Euphorbiodendron* Millspaugh (1909: 305).

*Ctenadena* Prokhanov (1933: 28).

*Sclerocyathium* Prokhanov (1933: 30).

SUBGENERA:

*Euphorbia* sg. *Esula* Persoon (1806: 14); type *Euphorbia Peplus* L. designated by Croizat (1939a: 13).

*Euphorbia* sg. *Keraselma* Necker ex Reichenbach (1928: 194); nomen nudum, based by implication on *Keraselma* Necker.

*Euphorbia* sg. *Tithymalus* Necker ex Reichenbach (1828: 194); nomen nudum, based by implication, on *Tithymalus* as delimited by Necker.

*Keraselma* sg. *Esula* Rafinesque (1838a: 116); type *Euphorbia Esula* L. Rafinesque did not refer to Persoon on page 116 but did mention on page 111 that Persoon had divided *Euphorbia* into two subgenera, *Tithymalus* and *Esula*.

*Keraselma* sg. *Karuiles* Rafinesque (1838a: 116); type *Euphorbia exigua* L.



- Keraselma* sg. *Lathyris* Rafinesque (1838a: 116); type *Euphorbia Lathyris* L.  
*Tithymalus* sg. *Paralias* Rafinesque (1838a: 115); type *Euphorbia paralias* L.  
*Tithymalus* sg. *Pythiusa* [sic] Rafinesque (1838a: 116); type *Euphorbia Pithyusa* L.  
*Tithymalus* sg. *Tulocarpa* Rafinesque (1838a: 115); type *Euphorbia palustris* L.  
*Tithymalus* sg. *Tuloisia* Rafinesque (1838a: 115); type *Euphorbia verrucosa* [L.?] *Tithymalus* sg. *Xarakias* Rafinesque (1838a: 115); type *Euphorbia Characias* L.  
*Euphorbia* sg. *Tithymalus* Tourn. ex Reichenbach (1841: 193); nomen nudum.  
*Euphorbia* sg. *Tithymalus* Ascherson & Graebner (1898: 469); type, *Euphorbia Helioscopia* L.; defined, no reference to earlier use of the subgeneric name.  
*Tithymalus* sg. *Acrochordonocarpus* Prokhanov (1933: 81); substituted for *Tithymalus* sg. *Pythiusa* Raf. and consequently takes the same type.  
*Tithymalus* sg. *Chylogala* (Fourr.) Prokhanov (1933: 57); based on *Chylogala* Fourr.  
*Tithymalus* sg. *Epurga* Prokhanov (1933: 56); type *Euphorbia Lathyris* L.  
*Tithymalus* sg. *Holophyllum* Prokhanov (1933: 68); type *Euphorbia blepharophylla* C. A. Mey.  
*Tithymalus* sg. *Keraselma* (Neck.) Prokhanov (1933: 118); based on *Keraselma* Neck.  
*Tithymalus* sg. *Murtekias* (Raf.) Prokhanov (1933: 206); based on *Murtekias* Raf.  
*Euphorbia* sg. *Tithymalus* Jepson (1936: 424 in key); need not necessarily be taken as new.

## SECTIONS:

- Euphorbia* s. *Tithymalus* Roeser (1828: 412); type *Euphorbia Helioscopia* L. Webb & Berthelot (1844-1850: 244); Baillon (1858: 284).  
*Euphorbia* s. *Esula* (Roeser) Koch (1837: 630); based on *Euphorbia* sect. *Tithymalus* §*Esula* Roeser. Godron (1855: 85).  
*Euphorbia* s. *Tithymalus* Koch (1837: 627); type *Euphorbia Helioscopia* L.  
*Euphorbia* s. *Esula* Dietrich (1841: 226); type *Euphorbia Esula* L.; no reference to earlier uses of *Esula* as a section.  
*Euphorbia* s. *Balsamis* Webb & Berthelot (1844-50: 253); type *Euphorbia balsamifera* Ait.  
*Euphorbia* s. *Helioscopia* (Roeser) Godron (1855: 76); based on *Euphorbia* sect. *Tithymalus* §*Helioscopia* Roeser.  
*Euphorbia* s. *Lathyris* Godron (1855: 98); type *Euphorbia Lathyris* L.  
*Euphorbia* s. *Exstipulatae* Roeser ex Klotzsch (1856: 276); based on "E. exstipulatae" described but not intended as a name by Roeser (1824: 59); type *Euphorbia Helioscopia* L.  
*Euphorbia* s. *Esula* Haw. ex Baillon (1858b: 284); based on *Esula* Haw.  
*Euphorbia* s. *Galarhoeus* Haw. ex Baillon (1858b: 284); based on *Galarhoeus* Haw.  
*Tithymalus* s. *Esula* Roeser ex Klotzsch (1859: 252); based by implication on *Euphorbia* s. *Tithymalus* §*Esula* Roeser. Bubani (1897: 91).  
*Tithymalus* s. *Galarhoeus* [as *Calorrhoeus*] (Haw.) Kl. & Gke. ex Klotzsch (1859: 252); based on *Galarhoeus* Haw. Marsson (1869: 416).  
*Euphorbia* s. *Umbellatae* Engelmänn (1859: 191); nomen nudum.  
*Tithymalus* s. *Esula* Haw. ex Marsson (1869: 416); based by implication on *Esula* Haw.  
*Euphorbia* s. *Tithymalus* (Scop.) Boissier (1862: 10, 99); based on *Tithymalus* Scop.  
*Euphorbia* s. *Helioscopiae* Krombach (1875: 395); type *Euphorbia Helioscopia* L.  
*Euphorbia* s. *Cyparissiae* Krombach (1875: 396); type *Euphorbia Cyparissias* L.  
*Euphorbia* s. *Chamaebuxus* Lázaro (1896: 282); type *Euphorbia Chamaebuxus* Bern.  
*Euphorbia* s. *Lagascae* Lázaro (1896: 282 in key); type *Euphorbia Lagascae* Spreng.

- Euphorbia* s. *Paralias* Lázaro (1896: 282 in key); type *Euphorbia Paralias* L.  
*Euphorbia* s. *Peplus* Lázaro (1896: 282 in key); type *Euphorbia Peplus* L.  
*Euphorbia* s. *Pithyusa* Lázaro (1896: 282 in key); type *Euphorbia Pithyusa* L.  
*Tithymalus* s. *Apios* Bubani (1897: 106); nomen nudum; type *Tithymalus Helioscopia*, based on *Euphorbia Helioscopia* L.  
*Tithymalus* s. *Euphorbia* Gómez de la Maza (1897: 153); based on *Euphorbia* sect. *Tithymalus* (Scop.) Boiss.  
*Euphorbia* s. *Tithymalus* Pers. sensu Fiori (1901: 275); as misapplied by Fiori equals *Euphorbia* subg. *Esula* Pers.  
*Euphorbia* s. *Cataputiae* Boehmer ex O. Kuntze in Post & Kuntze (1904: 223); no species assigned; by definition obviously refers to *Euphorbia Lathyris* L.  
*Euphorbia* s. *Galarrhaei* Boiss. ex Pojero (1907: 337); based by implication on *Euphorbia* sect. *Tithymalus* §*Galarrhaei* Boiss.; defined. Pax (1921: 150).  
*Euphorbia* s. *Myrsiniteae* [as *Myrsinites*] Boiss. ex Pojero (1907: 345); based by implication on *Euphorbia* sect. *Tithymalus* §*Myrsiniteae* Boiss.; defined.  
*Euphorbia* s. *Esulae* Boiss. ex Pax (1921: 151); based by implication on *Euphorbia* sect. *Tithymalus* §*Esulae* Boiss.  
*Euphorbia* s. *Tenellae* Pax & K. Hoffmann in Pax (1921: 147); type *Euphorbia glauccella* Pax  
*Euphorbia* s. *Trichadenia* Pax (1921: 152); type *Euphorbia trichadenia* Pax. Hässler (1931: 318).  
*Tithymalus* sg. *Acrochordonocarpus* Prokh.: The three following are sections of T. sg. *A.*:  
*Microsphaeria* Prokhanov (1933: 117); type *Euphorbia microsphaeria* Boiss.  
*Pythiusa* (Raf.) Prokhanov (1933: 82); based on *Tithymalus* subg. *Pythiusa* Raf.  
*Tulocarpa* (Raf.) Prokhanov (1933: 94); based on *Tithymalus* subg. *Tulocarpa* Raf.  
*Tithymalus* sg. *Keraselma* (Necker) Prokh.: The six following are sections of T. sg. *K.*:  
*Conicarpus* Prokhanov (1933: 155); type *Euphorbia humilis* C. A. Mey.  
*Cymalospermum* Prokhanov (1933: 151); type *Euphorbia falcata* L.  
*Esula* Prokhanov (1933: 166); type *Euphorbia Buhsei* Boiss. (*E. Esula* L. was not included; this sect. was proposed without reference to any earlier use of *Esula*).  
*Herpetorrhiza* Prokhanov (1933: 142); type *Tithymalus polytmeticus* Prokhanov.  
*Oppositifolium* (Boiss.) Prokhanov (1933: 122); based on *Euphorbia* sect. *Tithymalus* §*Oppositifoliae* Boiss.  
*Pseudokeraselma* Prokhanov (1933: 119); type *Euphorbia Helioscopia* L.

## SUBSECTIONS:

- Euphorbia* sect. *Tithymalus* (Scop.) Boiss.: The following are all subsections of *E. s. T.*:  
*Carunculares* Boiss. ex Pax (1891: 109); based on *Euphorbia* sect. *Tithymalus* §*Carunculares* Boiss.  
*Crotonopsidae* Boiss. ex Pax (1891: 109); based on *Euphorbia* sect. *Tithymalus* §*Crotonopsidae* Boiss.  
*Decussatae* Boiss. ex Pax (1891: 109); based on *Euphorbia* sect. *Tithymalus* §*Decussatae* Boiss.  
*Esulae* Boiss. ex Pax (1891: 110); based on *Euphorbia* sect. *Tithymalus* §*Esulae* Boiss.  
*Galarrhaei* Boiss. ex Pax (1891: 110); based on *Euphorbia* sect. *Tithymalus* §*Galarrhaei* Boiss.

*Laurifoliae* Boiss. ex Pax (1891: 109); based on *Euphorbia* sect. *Tithymalus* §*Laurifoliae* Boiss.

*Myrsiniteae* Boiss. ex Pax (1891: 110); based on *Euphorbia* sect. *Tithymalus* §*Myrsiniteae* Boiss.

*Oppositifoliae* Boiss. ex Pax (1891: 109); based on *Euphorbia* sect. *Tithymalus* §*Oppositifoliae* Boiss.

*Osyrideae* Boiss. ex Pax (1891: 109); based on *Euphorbia* sect. *Tithymalus* §*Osyrideae* Boiss.

*Pachycladae* Boiss. ex Pax (1891: 109); based on *Euphorbia* sect. *Tithymalus* §*Pachycladae* Boiss.

*Tenellae* (Pax & K. Hoffm.) Pax & K. Hoffmann (1931: 218); based on *Euphorbia* sect. *Tenellae* Pax & K. Hoffm.

#### SERIES:

*Euphorbia* s. *Exappendiculatae* Boissier (1862: 70); included all the exappendiculate sections; for convenience *Euphorbia* sect. *Tithymalus* (Scop.) Boiss. is assigned as type. This was not a series in the proper sense since it was used as higher in rank than a section.

*Euphorbia* s. *Exstipulatae* Boissier (1879: 1083); nomen nudum; the exstipulate sections including sect. *Tithymalus* (Scop.) Boiss. which is assigned as type. This was not a series in the proper sense since it was used as higher in rank than a section.

#### MISCELLANEOUS CATEGORIES:

*Euphorbia* Tribu *Tithymalus* Mutel (1848: 550); type *Euphorbia Helioscopia* L.

*Euphorbia* Tribu *Tithymalus* Duchartre (1857: 45); not coordinate with sect. *Tithymalus* but rather intended to include all the non-succulent species.

*Euphorbia* Rotte *Esula* Ducommun (1869: 664); type *Euphorbia Esula* L.

*Euphorbia* Rotte *Helioscopia* Ducommun (1869: 664); type *Euphorbia Helioscopia* L.

*Euphorbia* Rotte *Lathyris* Ducommun (1869: 664); type *Euphorbia Lathyris* L.

#### CATEGORIES OF UNSPECIFIED OR UNCERTAIN RANK:

(Note: The following list is alphabetical except that under *Tithymalus* as a subdivision of *Euphorbia* first *Tithymalus* as a subgenus is listed, then as a section, then as of unknown rank.)

*Esula* \**Annuae* Haworth (1812: 156); type *Esula Peplus* (L.) Haw., based on *Euphorbia Peplus* L.

*Esula* \**Suffrutescentes* Haworth (1812: 153); type *Esula dendroides* (L.) Haw., *Euphorbia Cyparissias* L.

*Esula* \**Suffrutescentes* Haworth (1812: 153); type *Esula dendroides* (L.) Haw., based on *Euphorbia dendroides* L.

*Euphorbia* l. *Balsamis* Webb ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Euphorbia* sect. *Balsamis* Webb & Berthelot.

*Euphorbia* \**Cataputiae* Bertoloni (1842: 95); type *Euphorbia Lathyris* L.

*Euphorbia* \**Characiae* Bertoloni (1842: 97); type *Euphorbia Characias* L.

*Euphorbia* h. *Characias* Gray ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Characias* S. F. Gray.

*Euphorbia* a *Galarhoeus* Haw. ex Schübler & Martens (1834: 297); based by implication on *Galarhoeus* Haw.

*Euphorbia* b *Esula* Haw. ex Schübler & Martens (1834: 297); based by implication on *Esula* Haw.

*Euphorbia*, *Esula* (Roepert) Döll (1843: 280); based by implication on *Euphorbia* sect. *Tithymalus* §*Esula* Roepert.

- Euphorbia* g. *Esula* Haw. ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Esula* Haw.
- Euphorbia* l. *Exstipulatae* Ledebour (1833: 179); type *Euphorbia* *Cyparissias* L.
- Euphorbia* f. *Galarhoeus* Haw. ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Galarhoeus* Haw.
- Euphorbia* n. *Lathyris* Godron ex Pfeiffer (1870: 309); nomen nudum, based by implication on *Euphorbia* sect. *Lathyris* Godron.
- Euphorbia* sect. *Stachydium* §*Capensis* Boissier (1862: 66); type *Euphorbia* *phylloclada* Boiss. Relationships dubious, Pax (1889: 35), in describing the synonymous *E. hereroensis*, placed it in *Euphorbia* sect. *Tithymalus*, i. e., subg. *Esula*, but Brown (1915: 255), described the glands as appendiculate which would exclude it.
- Euphorbia* \**Tithymali* Bertoloni (1842: 42); type *Euphorbia* *Esula* L.
- Euphorbia* subg. *Tithymalus* Reichb. b. *Esula* Haw. ex Reichenbach (1841: 193); nomen nudum, based by implication on *Esula* Haw.
- Euphorbia* subg. *Tithymalus* Reichb. a. *Galarhoeus* Haw. ex Reichenbach (1841: 193); nomen nudum based by implication on *Galarhoeus* Haw.
- Euphorbia* sect. *Tithymalus*: The following twenty-five indented names are subdivisions of *E. s. T.*:
- §*Carunculares* Boissier (1862: 111); type *Euphorbia* *serrata* L.
- A. *Cataputiae* Bertoloni ex Fiori (1901: 275 in key); based by implication on *Euphorbia* \**Cataputiae* Bertoloni.
- D. *Characiae* Bertoloni ex Fiori (1901: 275 in key); based by implication on *Euphorbia* \**Characiae* Bertoloni.
- §*Crotonopsidae* Boissier (1862: 101); type *Euphorbia* *lanata* Sieber ex Sprengel.
- §*Decussatae* Boissier (1862: 99); type *Euphorbia* *Lathyris* L.
- C. *Denudatae* Fiori (1901: 275 in key); type *Euphorbia* *Helioscopia* L.
- C. *Denudatae* a *Annuae* Fiori (1901: 281 in key); type *Euphorbia* *Helioscopia* L.
- C. *Denudatae* b *Perennes* Fiori (1901: 281 in key); type *Euphorbia* *dendroides* L.
- §*Esula* Roeser (1828: 414); type *Euphorbia* *Esula* L.
- †*Esula* Haw. ex Webb & Berthelot (1844-50: 245); nomen nudum, based by implication on *Esula* Haw.
- §*Esulae* Boissier (1862: 138); type *Euphorbia* *Esula* L.
- §*Galarrhaei* Boissier (1862: 113); type *Euphorbia* *Helioscopia* L.
- §*Helioscopia* Roeser (1828: 413); type *Euphorbia* *Helioscopia* L.
- †*Helioscopiae* Webb & Berthelot (1844-50: 244); type *Euphorbia* *Helioscopia* L.
- §*Laurifoliae* Boissier (1862: 105); type *Euphorbia* *laurifolia* Juss. in Lam.
- §*Myrsinitae* Boissier (1862: 173); type *Euphorbia* *Myrsinites* L.
- B. *Ornatae* Fiori (1901: 275 in key); type *Euphorbia* *palustris* L.
- B. *Ornatae* b *Annuae* Fiori (1901: 276 in key); type *Euphorbia* *platyphylla* L.
- B. *Ornatae* a *Perennes* Fiori (1901: 276 in key); type *Euphorbia* *palustris* L.
- §*Oppositifoliae* Boissier (1862: 99); type *Euphorbia* *pygmaea* F. & M.
- §*Oppositifoliae* \**Carunculatae* Boissier (1862: 99); nomen nudum, type *Euphorbia* *pygmaea* F. & M.
- §*Oppositifoliae* \**Ecarunculatae* Boissier (1862: 200); nomen nudum, type *Euphorbia* *Turczaninowii* Kar. & Kiril.
- §*Oxyrideae* Boissier (1862: 107); type *Euphorbia* *oxyridea* Boiss.
- §*Pachycladae* Boissier (1862: 107); type *Euphorbia* *dendroides* L.
- \**Sparsifoliae* Parlatores (1869: 455); type *Euphorbia* *palustris* L.
- Euphorbia* B. *Tithymalus* Reichenbach (1832: 755); type *Euphorbia* *Helioscopia* L.
- Euphorbia* B. *Tithymalus* a. *Galarhoeus* [as *Galarrhoeus*] Haw. ex Reichenbach (1832: 755); based by implication on *Galarhoeus* Haw.

*Euphorbia* B. *Tithymalus* b. *Keraselma* Necker ex Reichenbach (1832: 759); based by implication on *Keraselma* Necker.

*Euphorbia*, [?] *Tithymalus* Döll (1843: 279); type *Euphorbia Helioscopia* L.

*Galarhoeus* \**Annui* Haworth (1812: 151); type *Galarhoeus Helioscopia* (L.) Haw., based on *Euphorbia Helioscopia* L.

*Galarhoeus* \**Glauci* Haworth (1812: 143); type *Galarhoeus Lathyris* (L.) Haw., based on *Euphorbia Lathyris* L.

*Galarhoeus* \**Perennes* Haworth (1812: 145); type *Galarhoeus palustris* (L.) Haw., based on *Euphorbia palustris* L.

4i. EUPHORBIA: possible synonyms of uncertain identity:

GENERA:

*Euphorbiopsis* Léveillé (1911: 446).

*Desmonema* Rafinesque (1833: 177).

5. CALYCOPEPLUS Planchon (1861: 30).

SECTION:

*Euphorbia* s. *Calycopeplus* (Planch.) Boissier (1862: 11, 175); based on *Calycopeplus* Planch.

6. ELAEOPHORBIA Stapf (1906a: T. 2823, & 1906b: 646).

CATEGORIES OF UNCERTAIN OR UNSTATED RANK:

*Euphorbia* sect. *Diacanthium* "Gruppe" *Grandifoliae* Berger (1906: 30, 34), type *Euphorbia drupifera* Schum. & Thonn.; chosen since the group was apparently named for *Euphorbia grandifolia* Haw. which was cited as a synonym of *E. drupifera*.

*Euphorbia* sect. *Euphorbium* subsect. *Diacanthium* §*Grandifoliae* (Berger) Pax & K. Hoffmann (1931: 215); based on the next above.

7. SYNADENIUM Boissier (1862: 187).

CATEGORY OF UNSTATED AND UNKNOWN RANK:

*Euphorbia*, *Synadenium* (Boiss.) Baillon (1863: 142); based on *Synadenium* Boiss.

8. MONADENIUM Pax (1894: 126).

GENUS:

*Lortia* Rendle (1898: 29).

9. STENADENIUM Pax (1901: 343).

10. PEDILANTHUS Necker (1790: 354).

GENERA:

*Tithymalus* Miller (1754: *Tithymalus*).

*Tithymaloides* Ortega (1783: 28); Post & O. Kuntze (1904: 562) as *Tithymalodes*.

*Ventenatia* Trattinnick (1802: 86).

*Crepidaria* Haworth (1812: 136).

*Tirucalia* Rafinesque (1838a: 112) in part.

*Diadenaria* Klotzsch & Garcke in Klotzsch (1859: 254).

*Hexadenia* Klotzsch & Garcke in Klotzsch (1859: 253).

*Cubanthus* (Boiss.) Millspaugh (1913: 371).

SUBGENERA:

*Euphorbia* subg. *Crepidaria* Haw. ex Reichenbach (1841: 193); nomen nudum based by implication on *Crepidaria* Haw.

*Euphorbia* subg. *Tithymalus* (Miller) House (1924: 472); based on *Tithymalus* Miller

but applied erroneously by House as equaling *Euphorbia* sect. *Tithymalus* (Scop.) Boiss.

#### SECTIONS:

*Euphorbia* sect. *Crepidaria* Haw. ex Baillon (1858b: 284); based on *Crepidaria* Haw. It appears that Baillon erred for he cited (1858b: 287) *Crepidaria* as a synonym of *Pedilanthus*.

*Pedilanthus* sect. *Cubanthus* Boissier (1862: 7); type *Pedilanthus linearifolius* Griseb. *Pedilanthus* sect. *Eupedilanthus* Boissier (1862: 4); based on *Pedilanthus*.

*Pedilanthus* sect. *Calceolastrum* Boissier (1866: 1261); type *Pedilanthus Finkii* Boiss.

*Pedilanthus* sect. *Anomalus* Millspaugh (1896: 305); type *Pedilanthus itzaeus* Millsp.

*Tithymaloidea* sect. *Pedilanthus* Gomez de la Maza (1897: 154); based on *Pedilanthus* sect. *Eupedilanthus* Boiss.

*Tithymaloidea* sect. *Cubanthus* Boiss. ex Post & Kuntze (1904: 562); based on *Pedilanthus* sect. *Cubanthus* Boiss.

*Tithymaloidea* sect. *Diadenaria* (Kl. & Gke.) O. Kuntze in Post & Kuntze (1904: 562); based on *Diadenaria* Kl. & Gke.

*Tithymaloidea* sect. *Eutithymaloidea* O. Kuntze in Post & Kuntze (1904: 562); based on "(*Eupedilanthus* Boiss.)," i.e., *Pedilanthus* sect. *Eupedilanthus*.

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## 6. Index to Tribes, Genera, and Their Subdivisions

In this index only the last name of any combination appears, e. g., for *Euphorbia* subg. *Aklema* sect. *Dichilium*, subsect. *Dichilium*, subsect. *Stormieae*, only *Stormieae* is indexed. Authors of names are given only where absolutely necessary in order to avoid ambiguity, as for *Esula* and *Tithymalus*. After a given name its rank or ranks is/are indicated by the following abbreviations: f family, tr tribe, str subtribe, g genus, sg subgenus, s section, ss subsection, se series, m miscellaneous categories, ? rank unknown. Finally a reference symbol such as A for Euphorbiaceae tribe Euphorbieae, or 4a for the first subgenus under the fourth genus (*Euphorbia* subg. *Chamaesyce*) is given to indicate the identity of the name in question and its place in the immediately preceding phylogenetic synopsis of the nomenclature. Under each of the ten valid genera, subdivisions are listed in order of rank, then chronologically, except names of unknown rank which are listed alphabetically.

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 Aculeatae s, 4f  
 Adenopetalum *σ*, sg, s, 4b  
 Adenorima g, 4h  
 Agaloma g, sg, 4b  
 Aklema g, sg, 4b  
 Alektorocotonum g, s, ss, 4b  
 Allobia g, 4h  
 Alskebra sg, 4f  
 Americanae ?, 4b

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 Anisophyllae tr, A  
 Anisophyllon s, 4a  
 Anisophyllum g, sg, s, m, 4a  
 Annuae Haw. ?, 4h  
 Annuae Fiori ?, 4h  
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 Anthacantha g, s, ss, 4f  
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 Apios s, 4h  
 Appendiculatae se, 4a  
 Aplanina g, sg, 4a  
 Arthrohamnus g, s, ss, ?, 4f  
 Athymalus g, sg, 4f  
 Balsamis s, ?, 4h  
 Biaculeatae ?, 4f  
 Bojeria g, 4f  
 Bongium s, 4d  
 Buxifoliae ?, 4a  
 Calceolastrum s, 10  
 Calycoplepus g, s, 5  
 Capensis ?, 4f  
 Carunculares ss, ?, 4h  
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 Cataputiae s, 4h  
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 Cereis s, ?, 4f  
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 Cheirolepidium s, ss, 4d  
 Cheloneae ss, ?, 4a  
 Chylogala g, sg, 4h  
 Compressae ?, 4f  
 Conicarpus s, 4h  
 Cordifoliae ?, 4a  
 Crepidaria g, sg, s, 10  
 Crossadenia s, ss, 4b  
 Crotonopsidae ss, ?, 4h  
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 Cubanthus g, s, 10  
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 Cymatospermum s, 4h  
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 Decussatae ss, ?, 4h  
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 Diacanthium s, ss, 4f  
 Diadenaria g, s, 10  
 Dichilium s, ss, 4b  
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 Dichotomae ?, 4a  
 Dichrophyllum g, 4b  
 Dichylum g, 4b  
 Diplocyathium g, 4h  
 Ditritra g, 4a  
 Ecarunculatae ?, 4h  
 Echinocactoides ?, 4f  
 Elaeophorbia g, 6  
 Elegantes ss, ?, 4a  
 Endosila g, 4a  
 Ephedromorpha s, 4b  
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 Esula Morandi g, 4f  
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 Goniostema s, ss, ?, 4f  
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 Helioscopia s, m, ?, 4h  
 Helioscopiae s, ?, 4h  
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 Osyridea ss, ?, 4h  
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 Tekeanae s, 4f  
 Tenellae s, ss, 4h  
 Tetracanthae ss, ?, 4f  
 Tirucalia g, 4f  
 Tirucalli s, ss, 4f  
 Tithymalae str, A  
 Tithymaleae tr, ?, A  
 Tithymali ?, 4h  
 Tithymalodes g, 10  
 Tithymaloides g, 10  
 Tithymalopsis g, s, ss, 4b  
 Tithymalus Miller g, sg, 10  
 Tithymalus [Tourn.], Trew, Hill, Adan-  
 son, Scopoli, et al. g, sg, s, m, ?, 4h  
 Tithymalus Persoon sg, 4f  
 Torfasadis g, 4f  
 Tracynae ?, 4a  
 Treisia g, sg, s, ss, ?, 4f  
 Triacanthae ss, ?, 4f  
 Triaculeatae ?, 4f  
 Trichadenia s, 4h  
 Trichosterigma g, sg, s, ss, ?, 4b  
 Trigonae m, ?, 4f  
 Tulocarpa sg, s, 4h  
 Tuloisia sg, 4h  
 Tumalis g, 4f  
 Umbellatae s, 4h  
 Vallaris g, 4b  
 Ventenatia g, 10  
 Xamesike g, sg, 4a  
 Xamobala sg, 4a  
 Xarakias sg, 4h  
 Zalitea g, 4b  
 Zygothylidum g, sg, s, ss, 4b

## Kelsey Locust, *Robinia kelseyi* Hort. ex Hutchins.

William A. Dayton

Although the literature on this ornamental plant is now extensive, as the appended bibliography tends to attest, considerable confusion or ignorance still appears to exist with regard to: (1) The botanical author of the species; (2) the date of its introduction into cultivation; (3) its habit, whether arborescent or frutescent or both; (4) its type locality, and (5) its precise relationship to other closely related species. The purpose of this paper is an endeavor to clarify these matters so far as may be possible at this time.

1. *Botanical author*.—It seems to be unanimously agreed that this species was both discovered and introduced into cultivation by Mr. Harlan P. Kelsey, now of East Boxford, Mass. (6, 7, 9, 11, 12, 13, 19, 24). The first published reference to *Robinia kelseyi* appears to have been Mr. Kelsey's nursery catalog for 1900-1901 (10, p. 9), which gives no botanical author for the species and the comment is confined to the statement "New species, now offered for the first time." The second printed reference to this plant appears to be Kelsey's 1902 catalog (11, p. 22), where again no author is given, and this comment is made: "Alleghany Moss Locust. New species. 2.5 ft. Introduced by us, and a fine variety with leaves much like the yellow locust and bright pink cluster of flowers. A distinct and valuable addition." The third printed reference is by Dr. John F. Cowell, Director of the Buffalo Botanical Garden (6, p. 1537) in Bailey's "Cyclopedia of American Horticulture"; here again is no mention of botanical authority, and a quotation (with no reference to its source), "'a new species discovered and introduced in 1901 by Harlan P. Kelsey. The bark much resembles *R. Pseudacacia* and the plant is sparingly pubescent. It is a compact shrub of distinct habit.'" The late W. W. Ashe in 1903 (3) developed the treatment of the genus *Robinia* for the Southeastern States in Small's Flora but failed to mention *Robinia kelseyi*. The fourth printed reference to this locust did not appear until 1907, when C. K. Schneider (19, p. 85) mentions the plant in a footnote, adding pessimistically "Ganz unklar blieb mir *R. Kelseyi*, von der Cowell, in Bail.", and quoting Cowell's quotation mentioned above. Not until Hutchinson's detailed notes appeared in 1908 (9, tab. 8213) is there anything approaching an adequate description of the species.

*Robinia kelseyi* was probably named by Mr. Kelsey for himself, a practice common among nurserymen, but not observed by botanists. At least seven different citations of authority for this species are given in botanical literature: (a) Rehder (16), in 1935 cited Bean as the author; (b) Henry, Koehne, Nash, Rydberg, Small, and Van Dersal (8, 12, 13, 18, 21, 22) cite Cowell; (c) Schneider (19, 20) cites "Cowell in Bail."; (d) Hutchinson (9), "Hort., ex Cowell in Bail."; (e) Index Kewensis (14), "Hort. ex Gard. Chron."; (f) Ashe (4) gives "Cr." as the author (a typographical error for Cowell??),

and (g) Rehder in 1934 and 1940 (15, 17) and Whitaker (24) give Hutchinson as the author. The use of Bean's name as author of *Robinia kelseyi* appears to be a mere *lapsus calami*. It is difficult to justify citation of Cowell as the author, because he appears to make no pretense of being such, and the (botanically quite inadequate) description he gives he puts in quotes as gotten from somebody else. In short, the name *Robinia kelseyi* appears definitely to have originated in horticulture, and Hutchinson was the first adequately to describe it botanically. Hence, under Article 48 of International Rules, the correct citation of this species appears to be *Robinia kelseyi* Hort. ex. Hutchins. or, "if desirable or necessary to abbreviate," *R. kelseyi* Hutchins.

2. *Date of introduction.*—Cowell's statement (6) that this species was introduced in 1901 by Harlan P. Kelsey is usually followed in the literature. However, Whitaker's statement (24) that Kelsey introduced the plant in 1900 seems to be correct; at least it agrees with the inference contained in Kelsey's catalog (10).

3. *Habit.*—*Robinia kelseyi* is usually referred to in literature as "shrubby," a "shrub," "compact shrub," "spreading shrub," or "frutex" (1, 2, 3, 4, 6, 9, 11, 13, 15, 16, 17, 18, 19, 21, 22, 24). Mr. Kelsey tells me he has never seen it in its native state or in his nursery except as a shrub. In a letter to me dated December 28, 1942, he adds this further information:

In *restricted places*, among other shrubs it has reached 12 ft. in our nursery grounds, otherwise I have never seen it over 10 feet in height, and I have been growing it now for 41 years. In any planting it spreads with great rapidity by underground roots, and it doesn't seem as though anything would stop it. This isn't in its favor, but a big mass of it in bloom is a very lovely sight. x x The x pods are covered with very dense hair, and it is a very prolific seeder.

However, the habit illustration in the Journal of the Royal Horticultural Society (2, fig. 134) shows a single-stemmed, excurrent, arborescent growth form. Koehne (12) indicates that the species may be a small tree — "Sträuchlein, oder kleiner 1-3 m. hoher Baum." Schneider (20) calls it a "kleines Bäumchen, 1-3 m." It may be significant that Wever omits this species from his paper on "bol" robinias (23). Whitaker (24), though listing Kelsey locust as "shrubby," refers to "its upright habit of growth." But there is also the definite evidence of Gibbs (7), who refers to the species twice as a "tree" and says "I own a flourishing tree on its own roots, 15 feet high with a girth of 6 inches and a spread of 10 feet" — the implication is that it is still growing. Furthermore, a recent specimen of *Robinia kelseyi*, collected by Mr. Jesse H. Buell of the Appalachian Forest Experiment Station, U.S. Forest Service, at 2600 feet in Yancey County, N. C., on the Pisgah National Forest (Buell no. 288, Forest Service serial no. 89365) is annotated (in part) with the collector's comment "Tree 12-15 ft. high." There seems to be no reasonable doubt but that *Robinia kelseyi* may properly be listed among the native arborescent species of the United States. The U.S. Forest Service is concerned with this matter, inasmuch as Dr. E. L. Little, Jr., Dendrologist of that bureau, is now revising Sudworth's "Check List" (published in 1927), in which work *Robinia kelseyi* does not appear.

4. *Type locality*.—The first reference to the type locality of *Robinia kelseyi* appears to be in 1912 by Henry (8, p. 1508), who says that the plant<sup>1</sup> originated "in the H. P. Kelsey's Nursery at Boston, U.S.A." In footnote 3 (*loc. cit.*) Henry further states: "Mr. Kelsey in a letter to Kew says that it came up spontaneously in his nursery; but supposes that it may have come into his collection with seed of other plants from the southern Alleghany Mountains." But in 1916 Nash (13) quotes from a "letter recently received from Mr. Kelsey in response to a request for information as to the locality and habitat of this plant." The quotation (in part) follows: "*Robinia kelseyi* was found growing on the Blue Ridge range south of Pineola, North Carolina. Its range so far as I know it is not wide, although very possibly it might be found in other places. x x x The altitude is about 3700 to 3900 feet elevation." Pineola, incidentally, is in Avery County, a few miles due north of the McDowell County boundary and a few miles east of Mitchell County line. In a letter to me dated November 29, 1939, Mr. Kelsey is even more specific; he says (in part): "The type locality where I discovered *Robinia kelseyi* was in Mitchell County on Rough Ridge, perhaps three miles from Pineola, North Carolina. The plants from which the description<sup>2</sup> was made were, I believe, sent by me to the New York Botanical Garden. All of my material of this species, which I have an abundance of, came from the same locality and may be called true type specimens."

It seems clear that the type locality of *Robinia kelseyi* is not Mr Kelsey's former nursery in Salem, Mass., but Rough Ridge, Mitchell County, N. C., about 3 miles or so east and south of Pineola, Avery County. Botanically speaking, this writer knows of no designated type specimen of *Robinia kelseyi*. Perhaps a sheet in the Kew herbarium should be so designated. There is no material of the species in the U. S. National Herbarium. Doubtless plants in cultivation are living isotypes, as Mr. Kelsey intimates.

5. Ashe Rehder, Rydberg, Schneider, Small, and Whitaker have published (3, 4, 15, 17, 18, 19, 21, 24) keys for all or part of the Southeastern shrubby locusts, but still the data on these plants are confusing and knowledge regarding their precise relationships is unsatisfactory. Ashe's numerous segregates, in particular, need further study. All the species in this complex should, if possible, be carefully studied by the same person in their respective type localities, and the type specimens (where these exist and can be located) thoroughly examined. Meanwhile, it may be suggestive and conducive to

<sup>1</sup> Henry considered this species to be "probably a hybrid between *R. hispida* and *R. pseudoacacia*." This theory is pretty thoroughly exploded. Whitaker (25, p. 354) refers to *R. kelseyi* as a "basic diploid species," with 10 pairs of chromosomes. *R. hispida* is a triploid, with 15 chromosome pairs; it has the highest recorded percentage of pollen sterility in the genus (88 per cent) and is propagated vegetatively, seldom producing pods or viable seed.

<sup>2</sup> Doubtless Mr. Kelsey refers to Nash's description in 1916 (13); Nash says the N. Y. Botanical Garden purchased two specimens of *Robinia kelseyi* in 1903 from Mr. Kelsey. The original description by Mr. Hutchinson of Kew Gardens in 1908 (9) was evidently based (see Bean, 5) on material purchased by Kew from Mr. Kelsey also in 1903.

further study to present some notes from the U. S. Forest Service range plant and dendrological herbarium, where material occurs of four of the species in this complex, all identified (or check-identified) by Dr. Frederick J. Hermann of the Bureau of Plant Industry.

In a memorandum, dated January 27, 1941, to Dr. Miriam L. Bornhard of the Forest Service, Dr. Hermann comments on Buell's no. 288 (Forest Service serial no. 89365), *Robinia kelseyi*, from the Pisgah National Forest as follows:

I find upon referring to my copy of Small that I had made a note therein to the effect that *Robinia Kelseyi* was probably not distinct from *R. Boyntonii*, and I suspect this was the origin of my original reference of this collection to *R. Boyntonii*. I should, however, have made a note to that effect on the annotation label.

After comparison of this specimen with the material available in the National Herbarium it seems to me that *R. Kelseyi* and *R. Boyntonii* have been pretty generally misinterpreted in the past, probably due to the inadequacy of the description of the two in the current manuals and to emphasis upon key characters which in reality are highly unstable.

It appears to me from a study of the six available collections of this complex, as well as from the various published descriptions of the two plants which are contradictory on so many points, that the presence or absence of stipular spines (in both species they tend to be more or less developed on the old wood, but are generally lacking altogether on the year-old branches and those of the season's growth, often the only wood to be found on herbarium specimens) and the degree of glandularity of the peduncles, are equivocal characteristics which are of no value in distinguishing between the two plants. The most reliable distinction between the two I think lies in the calyx lobes: in *Boyntonii* these are short and abruptly acute to abruptly short-acuminate, in *Kelseyi* they are narrower, longer and long-caudate, so that in their total length the lobes exceed the calyx tube. There is a hint of this character in the description by Rehder and that by Rydberg in North American Flora, otherwise it seems to have been overlooked. The other character which has some appearance of stability is the difference in leaflet shape: elliptic-ovate in *Boyntonii*, elliptic-lanceolate to elliptic-oblong in *Kelseyi*, but this distinction is somewhat relative.

A composite key to the four species referred to, subject to correction or emendation as a result of hoped-for future study of types and type localities, may be framed about as follows:

Twigs glabrous or at first puberulent, not hispid, glandular or viscid. Calyx glandular-pubescent; pods glandular-hispid with purplish hairs.

Calyx-lobes ovate or lance-ovate, shorter than the tube. Leaflets of an elliptic or elliptic-ovate type, pubescent at first; flowers pink, rose-purple or whitish, about 17-20 mm. long, in rather loose, 8- to 12-flowered racemes. .... Boynton Locust, *Robinia boyntonii* Ashe

Calyx-lobes narrow, often (especially the lowest one) caudate, longer than the tube. Leaflets lanceolate, elliptic-lanceolate, or elliptic-oblong; flowers rose-colored, 15-25 mm. long, in 5- to 8-flowered racemes. .... Kelsey Locust, *R. kelseyi* Hort. ex Hutchins.

(N.B. Ashe's attribution of smaller flowers to *kelseyi* than to *boyntonii* seems questionable. Separation of these two species on the basis of glabrous vs. glandular peduncles (and of stalked vs. stalkless glands) also appears dubious).

Twigs glandular, viscid, or hispid. Pods glandular-hispid (though seldom formed in *R. hispida*).

Twigs hispid, not glandular-viscid, the twig-bristles 3-5 mm. long.

Plant a stoloniferous shrub, typically up to 1 m. high; leaflets 7-13, suborbicular to broad-oblong, 20 to 35 mm. long, usually glabrous, rounded and mucronulate at apex. Flowers 20-25 mm. long, often with a pale-purplish or bluish cast, in 3- to 5-flowered racemes; rachises, peduncles, and pedicels hispid. ....Roseacacia Locust, *R. hispida* L.  
(N.B. The var. *R. hispida rosea* Pursh (= *R. grandiflora* Ashe) is a more luxuriant, much more sparingly hispid state of this species).

Twigs glandular-viscid ("clammy"), not hispid.

Plant a shrub 4-8 ft. high to tree size, as much as 40 ft. high; leaflets 13-25, lance-ovate to ovate, 20-40 mm. long, obtuse or acute at apex, broad-cuneate at base, mostly pubescent beneath. Flowers about 20 mm. long, pink with yellow blotch on standard, in 6- to 16-flowered racemes; bracts conspicuous, longer than calyx; calyx reddish-pubescent; glands on twigs and peduncles subsessile; pods sparingly glandular-hispid. ....Clammy Locust, *R. viscosa* Vent.

Fig. 1 shows comparable floral parts, on the same scale, of *Robinia boyntonii*, *R. hispida*, *R. kelseyi*, and *R. viscosa*, drawn by Miss Leta Hughey of the U. S. Forest Service from material check-identified by Dr. Frederick J. Hermann of the Bureau of Plant Industry. It is hoped that this may prove of some service in connection with necessary future study of these and related species. The illustrations indicate certain apparent tendencies in indument and shape and relative length of calyx-lobes. Whether such apparent characters as the relative depth of the keels of *hispida* and *kelseyi*, indentation of standard

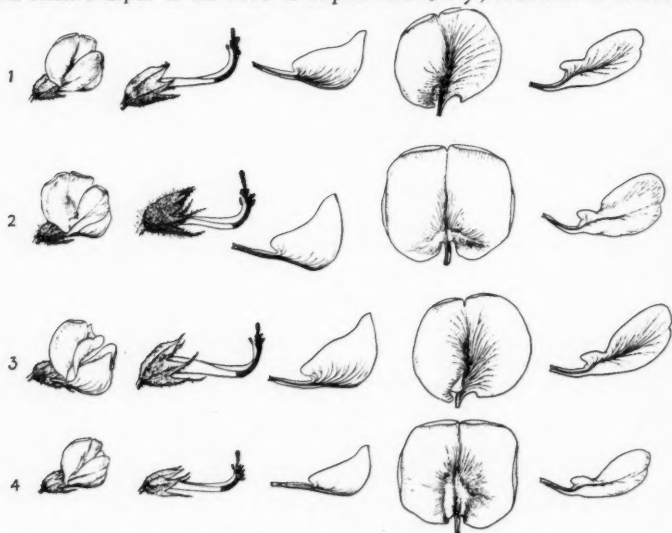


Fig. 1. From left to right, in order: Flower (cir.  $\times 1/3$ ); calyx with stamens and pistil (cir.  $\frac{1}{2}$  nat. size); keel (cir. nat. size); standard (cir.  $\frac{1}{2}$  nat. size), and wing (cir.  $\frac{1}{2}$  nat. size) of (1) *Robinia boyntonii*, (2) *R. hispida*, (3) *R. kelseyi*, and (4) *R. viscosa*.

base in *hispida*, and relative narrowness of wing of *boyntonii* and *viscosa* are sufficiently stable to have any diagnostic value remains for future investigation of this obscure and difficult group.

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## Osteology of the Skull of *Cnemidophorus*

Ernest Paul Du Bois

With the increasing interest of vertebrate paleontologists in the group of "mammal-like reptiles" it has become evident that there is further need of detailed morphologic studies of the related group. With this in mind, a series of studies aimed at a comprehensive description of the skull of *Cnemidophorus* was initiated. It is proposed at a later date to publish data on the soft parts of the head.

*Cnemidophorus* was chosen because of its generalized structure, its availability, and its small size, which permits the making of serial sections. Two species, *C. gularis* and *C. sexlineatus*, were used.

Acknowledgments for assistance in this study are due to Mr. Karl P. Schmidt of the Field Museum of Natural History, and to Dr. Everett C. Olson and Mrs. Sylvia Bensley, both of the University of Chicago.

### Detailed Analysis of the Bones

*Frontal*.—The frontal is an unpaired bone which extends from the posterior level of the orbits to a point slightly anterior of their forward limits. In cross section the dorsal surface is essentially flat anteriorly, slightly convex between the orbits, and somewhat concave posteriorly. Ornamentation is absent except on the hinder part which is slightly rugose. Anteriorly, the frontal is produced into three processes of about equal prominence. The middle process is inserted between the paired nasals, and the lateral ones between the nasals and prefrontals on each side. Posteriorly, the frontal meets the parietal in a prominent suture. The postero-lateral boundaries are wing-like and are clasped for a considerable distance by the postorbitals. From the ventral aspect, the frontal is flat posteriorly but arched upward anteriorly to allow the passage of the olfactory tracts.

*Parietal*.—The parietal is an unpaired bone, wider than long, extending from the frontal to the occipital region. The main body of the bone is rectangular, produced antero-laterally into a pair of small wings which articulate with the frontal and postorbital, and postero-laterally into a pair of elongate processes which meet the squamosal and the paroccipital process of the otooccipital. A small median notch exists in the rear border of the parietal. This notch is commonly closed by a sheet of connective tissue in which is imbedded a small cartilaginous element, possibly the homologue of the dermal-supraoccipital of other forms, or the remainder of the chondrocranial tectum synoticum. The posterior border of the parietal is flanged. Laterally, it is deflected downward over most of its length, forming a pair of lateral plates which partially enclose the sides of the brain. Anteriorly, these plates are some-

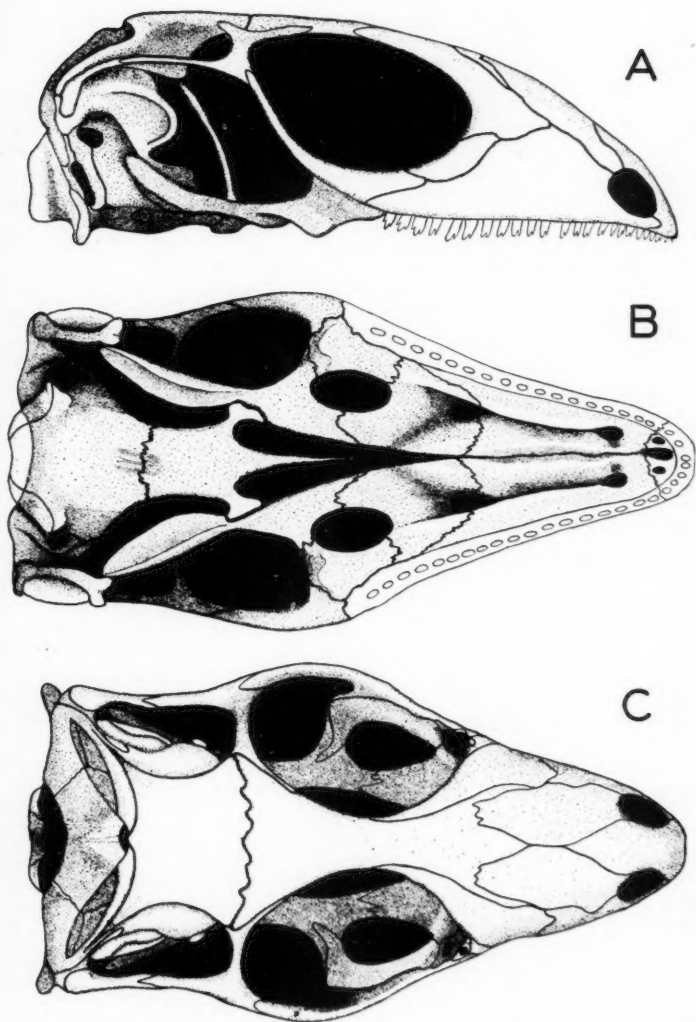


Fig. 1. Diagram ( $\times 9$ ) of skull of *Cnemidophorus* sp. showing (A) lateral, (B) ventral, and (C) dorsal aspects.

what more pronounced and receive the epipterygoids in a pair of poorly developed notches. A median ridge is present on the ventral side of the parietal, partially filling in the cerebral fissure. The entire dorsal surface is more or less rugose.

*Supraoccipital*.—The supraoccipital is a large median element lying between the parietal and the foramen magnum. It is united ventro-laterally with the oto-occipital and laterally with the proötic by well developed sutures. A poorly defined median ridge divides the supraoccipital into right and left halves. The posterior end of the anterior semi-circular canal and the medial end of the posterior semi-circular canal unite in the supraoccipital to form the crus communis. Their courses may be easily seen through the thin covering of bone.

*Oto-occipital* (*Parotic* and *paroccipital* of authors).—The oto-occipital bounds the foramen magnum laterally. It consists of the fused exoccipital and opisthotic. Traces of the sutures between these bones persist. The ventral portion of the posterior semi-circular canal is largely confined to the opisthotic but seems to enter into the exoccipital to an indeterminable extent. Laterally, the paroccipital process articulates by means of a cartilaginous element with the quadrate below and with the squamosal anteriorly. It meets a very attenuated portion of the parietal dorsally. The suture separating the oto-occipital from the proötic starts at the junction of the suture between the supraoccipital and oto-occipital with that between the supraoccipital and the proötic. It proceeds from this point postero-laterally to the union of the parietal arch and the paroccipital process, and then proceeds ventrally to the fenestra ovalis in front of the fenestra rotunda and finally terminates in an unossified zone between the basioccipital, opisthotic, and proötic. From this unossified zone, the suture dividing the basioccipital and oto-occipital may be traced posteriorly for a short distance. It then turns dorsally and terminates at the posterior border of the fenestra rotunda. The oto-occipital forms the ventral and posterior border of this opening. From the posterior border of the fenestra, the line of union swings around the basioccipital tubera and then medially across the back of the skull to the foramen magnum. The twelfth nerve exits by two openings in the exoccipital portion. The condyle is single and tripartite, the exoccipital forming its dorso-lateral portions.

*Basioccipital*.—The basioccipital forms the lower border of the foramen magnum and extends anteriorly to the basisphenoid. It is bounded laterally by the oto-occipitals and proötics. The antero-lateral margins are clasped by a pair of processes extending back from the basisphenoid. Near its posterior margin, the basioccipital exhibits a pair of strongly developed ventral processes, the basioccipital tubera, which extend laterally and posteriorly. A slight median ridge extends back from the basioccipital-basisphenoid suture for a distance equivalent to one-third of the length of the bone.

*Basisphenoid*.—The basisphenoid extends anteriorly from an irregular suture which separates it from the basioccipital. The basipterygoid processes are well developed and expanded distally at their junction with the pterygoids.

The parasphenoid<sup>1</sup> rostrum is membranous and easily lost during preparation. It extends far forward between the pterygoids and palatines. The sella turcica is pronounced as a result of the well developed dorsum sellae which forms its posterior wall. A slender process of the proötic lies alongside the basisphenoid and is suturally related to its lateral edges.

*Proötic*.—The proötics form the lateral walls of the brain case. Their structure and relationships are complex. Each proötic is divided by a well developed ridge which starts at the parietal arch and proceeds antero-ventrally to the proximal end of the basiptyergoid process. Anterior to this ridge the proötic consists of a vertical plate, in which lies most of the anterior semi-circular canal, and which articulates dorsally with the parietal and posteriorly with the supraoccipital and oto-occipital. Posterior to the ridge, the proötic is also plate-like but is oriented in a somewhat different plane. The posterior edge forms the border of the fenestra ovalis. Ventrally the proötic meets the basioccipital and basisphenoid.

*Quadrate*.—The quadrate lies ventral to the distal end of the paroccipital process from which it is separated by a cartilaginous pad. Each quadrate consists of a slightly recurved bony axis with a pair of wings on the lateral and medial sides so shaped that they, particularly the lateral one, resemble backward-facing cups. The lateral wing is considerably larger than the medial. The inner portion of the distal end of the quadrate is connected by means of a cartilaginous pad to the outer surface of the pterygoid. The distal end of the otostapes lies posterior to the main axis of the quadrate, to which it is bound by connective tissue.

*Pterygoid*.—The pterygoid extends from the ventral surface of the quadrate anteriorly to join the palatine with which there is sutural union. In general, the pterygoid is Y-shaped and consists of the quadrate process, posterior, and the palatine and ectopterygoid processes, anterior. A cartilaginous pad exists between the pterygoid and ectopterygoid. The quadrate process is flat but bears on its ventral surface a knife-like ridge which extends from the level of the basisphenoid union posteriorly to the end of the bone. The basiptyergoid process fits into an oblique groove on the pterygoid. The meniscus pterygoideus is present and moderately developed. The epiptyergoid arises from a depression on the dorsal surface at about the same level as the union with the basisphenoid. Three palatal teeth are present medially near the anterior end of each pterygoid.

*Ectopterygoid*.—The ectopterygoid lies antero-laterally to the ectopterygoid process of the pterygoid. It articulates with four bones: postero-medially with the pterygoid, postero-laterally with the jugal, antero-laterally with the maxil-

<sup>1</sup> Much confusion is present in the literature as to whether the process directed anteriorly from the basisphenoid is pre- or parasphenoid, some authors going so far as to use the terms synonymously. Their separate identity is easily established embryologically by their different antecedents and morphologically by the presence of both bones in many reptiles. The parasphenoidal identity of this process may be established embryologically, structurally, and paleontologically.

lary, and antero-medially with the palatines. An oval infra-orbital fossa is enclosed between the pterygoid, ectopterygoid, and palatine.

*Epipterygoid*.—The epipterygoid has been treated incidentally to the description of other bones. It is a rod-shaped structure extending from the pterygoid, in which it fits into a groove, to the parietal, in which it is received in a poorly defined notch.

*Palatine*.—The palatine extends anteriorly from the pterygoid to the vomer. Laterally, for a short distance, the palatine meets the ectopterygoid, and for a much longer distance, the alveolar surface of the maxillary. Anteriorly it is united by a suture to the vomer. Strongly developed depressions at the anterior ends of the palatines indicate the openings of the internal nares. The antero-medial edges of the palatines are prevented from meeting in the midline by a pair of posteriorly directed processes from the vomer.

*Vomer*.—Although in recent years this bone has been known as the "prevomer," in light of the recent researches of Parrington and Westoll,<sup>2</sup> the use of the early term seems advisable inasmuch as these authors have shown that the reptilian vomer is homologous to the mammalian vomer. The vomer in *Cnemidophorus* is formed of paired lateral members. Posteriorly, it joins the palatines, anteriorly, the maxillary and premaxillary. Small foramina on the antero-lateral edges of the vomer connect the buccal cavity with Jacobson's organ. In the prepared skull these foramina are confluent with the internal nares. There are no vomerine teeth.

*Septomaxillary*.—The septomaxillary is a thin plate which extends obliquely from the trabecula communis ventrally and laterally beneath the nasal passages to the lateral border of the vomer. It is not visible except in cross section.

*Premaxillary*.—The premaxillary is a median bone composed of fused lateral members. It articulates ventrally with the vomer, laterally with the maxillaries, and dorsally with the nasals, between which a long nasal process is inserted. Teeth are much reduced on the premaxillary.

*Maxillary*.—The maxillary forms most of the lateral surface of the anterior part of the skull. It articulates with the nasal, prefrontal, lacrimal, jugal, ectopterygoid, palatine, vomer, and the premaxillary, and forms a part of the border of the external nares. It is excluded from the infra-orbital fossa by the ectopterygoid. Each maxillary bears about 17 teeth which are pleurodont in their mode of attachment. The teeth are generally single-cusped, but frequently have a small subsidiary cusp anteriorly, and less frequently, posteriorly. The teeth are constantly replaced by others coming in at their base. Numerous nutrient foramina are present along the lateral margin of the maxillary.

*Jugal*.—The jugal is a relatively long curved bone which forms most of the lower margin of the orbit. Anteriorly, it articulates with the lacrimal and the

<sup>2</sup> F. H. Parrington and T. S. Westoll, "On the Evolution of the Mammalian Palate," *Phil. Trans. Roy. Soc. London, Series B*, 230:305-355, 1940.

maxillary. Posteriorly, articulation is with the fused postorbital-postfrontal. Ventrally, the jugal meets for a short distance the pterygoid and ectopterygoid.

*Squamosal*.—The squamosal has simple relationships. It is sliver-like, reaching from the postorbital-postfrontal in front, to the tabular behind. The posterior end is slightly flared. Approximately half of the lower border of the supratemporal fossa is formed by the squamosal.

The identity of the squamosal is related directly to the phylogenetic history of the lizards. Recent studies on *Youngina*, *Youngoides*, and other pro-lizard types seem to indicate quite clearly the origin of the Lacertilia from a diapsid stock. If this be the case, the only logical identity of the bone in question is squamosal.

*Tabular*.—The tabular is an elongate bone forming the antero-ventral border of the parietal arch. It is inserted between the squamosal, parietal, and oto-occipital. From this position it proceeds antero-medially along the ventral surface of the posterior process of the parietal.

*Postorbital-postfrontal*.—In *Cnemidophorus* the postorbital and postfrontal are fused into an X-shaped bone which separates the orbit from the supra-temporal fossa. It has two medial processes which clasp the frontal and parietal, and two lateral processes which articulate with the jugal and squamosal.

*Prefrontal*.—The prefrontal lies, as the name suggests, anterior and lateral to the frontals. It sends a process posteriorly along the medial border of the orbit. The nasals make slight contact with the bone; the maxillaries meet it over most of its anterolateral border. The lacrimal lies lateral to the prefrontal.

*Lacrimal*.—The lacrimal forms the border of the lower part of the anterior wall of the orbit. It meets the prefrontal dorsally, the jugal ventrally, and the maxillary anteriorly. Inside the orbit, the lacrimal sends a very pronounced plate medially, across the anterior orbital wall, nearly to the midline. This plate extends from the palatine below to the prefrontal above. In the ventro-lateral corner of this plate is the opening for the lacrimal duct.

*Nasal*.—The nasal extends from the posterior edge of the external naris posteriorly and medially to the frontal. The paired nasals meet in the midline for a short distance, but are separated anteriorly by a process from the premaxillary and posteriorly by a similar process from the frontal. Laterally, union is made with the prefrontal and maxillary.

*Stapes*.—The stapes is a rod-like bone which extends from the fenestra ovalis laterally to the posterior border of the quadrate. It is slightly swollen at both distal and proximal ends.

#### Detailed Analysis of the Foramina

*Lacrimal*.—The foramen through which the lacrimal duct passes is a relatively large opening situated between the medially deflected blade of the prefrontal and the lacrimal bone. The opening is crescent shaped with the

convexity directed laterally. Anteriorly, the maxillary replaces the lacrimal in forming the lateral boundary of the lacrimal canal. There is some indication of the double nature of the lacrimal duct in emarginations present on the dorsal and ventral margins of the crescent.

*Infraorbital*.—The infraorbital foramen, through which passes the superior alveolar branch of the fifth nerve, lies slightly ventral to the lacrimal foramen. It is bordered dorsally by the inflected portion of the prefrontal, medially by the palatine, and ventrally and laterally by a prolongation of the maxillary. In some cases the ectopterygoid may form a portion of its posterior border. A short distance anteriorly, the medial wall of the canal disappears and the foramen is replaced by a groove in the alveolar portion of the maxillary.

*Maxillary*.—Normally, five or six maxillary foramina are present on the lateral surface of each maxillary bone. They are arranged in an anterior-posterior row located immediately above the dental margin of that bone. These openings allow small twigs of the superior alveolar branch of the fifth nerve to pass out of the bone laterally and to supply innervation to the glandular tissues in the membranes of the upper lip. Small blood vessels generally accompany these twigs but are more irregular in their presence.

*Nasal*.—Usually, three small openings on each maxillary and about eight on each nasal indicate the places of exit of small terminal twigs of the rami nasalis medialis and lateralis. The lateralis twigs are restricted to the maxillary and the medialis to the nasal. There seems to be little regularity in the arrangement of these openings.

*Proötic incisure*.—The proötic incisure, while not strictly a foramen, is a very important landmark. It is located at the inferior-anterior margin of the proötic, immediately ventral to the genu of the anterior semicircular canal. It normally lodges the ganglion of trigeminal nerve.

*Abducens*.—The sixth nerve passes through a small foramen in the antero-lateral floor of the basisphenoid. The foramen courses forward in the upwardly deflected body of the bone, above the carotid canal, and appears again on the postero-lateral wall of the sella turcica.

*Carotid*.—The internal carotid artery maintains a ventro-anterior course over the external surface of the proötic bone and, in older specimens particularly, is protected by a projecting superjacent ledge of the proötic. Anteriorly the artery enters the body of the basisphenoid, with the palatine branch of the seventh nerve, at a level near that of the basioccipital-basisphenoid suture, and a short distance posterior to the proximal end of the basipterygoid process. The canal proceeds through the basisphenoid ventral to the abducens canal and enters the posterior wall of the sella turcica somewhat ventral and medial to the opening of the abducens.

*Facial*.—The root of the facial nerve penetrates the proötic immediately ventral to a larger opening which marks the anterior acoustic foramen. The external opening of the facial lies ventral to the oblique ridge which shelters



the carotid and in life is covered by the ganglion of the seventh nerve. From this ganglion, a palatine branch runs forward paralleling the carotid and entering the basisphenoid through the carotid canal. Within the basisphenoid, the carotid canal gives off a lateral branch through which passes the palatine nerve and a small accompanying blood vessel. The opening for the palatine nerve lies in the angle which the basipterygoid process makes with the basisphenoid.

*Acoustic.*—The medial aspect of the brain case exhibits several large foramina. Immediately dorsal to the facial foramen is a large opening, the anterior acoustic foramen, which marks the entrance of the anterior branch of the eighth nerve. A deep depression proceeds posteriorly from this opening and terminates in another large foramen, the posterior acoustic. Within this latter opening, in its roof, a minute foramen is present which transmits dorsally a small branch of the posterior auditory nerve.

*Endolymphatic.*—Some distance above the aforementioned complex lies a foramen through which passes the endolymphatic duct. It is located at the apex of a triangular boss, the base of which is marked by the foramina acustica and facialis.

*Rotunda and Cochleae.*—Ventral and posterior to the acoustic complex, a large perilymphatic canal passes out of the cranial cavity. Its outer opening, the fenestra rotunda, is covered by the secondary tympanic membrane. Dorsally, a well developed fenestra cochleae enters the perilymphatic canal and connects it with the vestibule of the ear. Externally, the fenestra rotunda is an elliptical opening immediately ventral to the fenestra ovalis and separated from it by a narrow blade of bone. The fenestra rotunda lies between the opisthotic and proötic.

*Ovalis.*—The fenestra ovalis is a more or less elliptical opening which lies dorsal to the fenestra rotunda. It is bordered along most of its dorsal, posterior, and ventral margin by the opisthotic and along its anterior margin by the proötic.

*Hypoglossal.*—Ventral and posterior to the fenestra cochleae, within the brain case, three small openings mark the passage of the several roots of the hypoglossal nerve. Externally, the roots of the hypoglossal are indicated by two small foramina lateral to the occipital condyle and ventral to the jugular foramen.

*Jugular.*—The jugular foramen is a large opening which lies above the external openings for the hypoglossal nerve. Within the brain case it lies posterior to the hypoglossal foramen.

*Pineal.*—The pineal body has no external opening but is lodged in a depression on the ventral side of the parietal.

## Elater-Bearing Spores from the Pennsylvanian Strata of Iowa\*

L. R. Wilson

In the course of paleobotanical studies of coal balls from the Des Moines Series in the Pennsylvanian strata of Iowa, numerous elater-bearing spores were discovered. A review of the literature on spores of this type showed that none are recorded from rocks earlier than the Triassic. The discovery is therefore significant in that it extends the record from the early Mesozoic Era back into the latter part of the Paleozoic Era. In addition, several interesting structural features are also shown by these Paleozoic spores.

Spores bearing elaters appear to be unique with the modern equisetalean family, Equisetaceae. This family today has one genus, *Equisetum*, with approximately twenty-five species. During the Mesozoic Era, the family appears to have had many representatives. The spores of these are imperfectly known. The other equisetalean family, the Calamariae, consists of extinct forms and none of these appear to have had elater-bearing spores.

The spores of the modern genus *Equisetum* are well known and have been studied in some detail by Knox (1938), who infers that elaters occur on all of the fifteen species examined. All have spherical spores, measuring 30 to 35 microns in diameter, and possess thin walls with no trace of a tri-radiate mark.

Macrofossils of *Equisetites* are abundant in the Mesozoic strata and spores have been isolated from the European Rhaetic and Triassic fossils by Halle (1908) and from the Triassic rocks of the southwestern United States by Daugherty (1941). Halle recorded the presence of a clearly visible trilete commissure on the spores but no trace of elaters was found. Halle's material was prepared by a maceration procedure and if elaters were present, they probably would have been removed by that process.

Daugherty in describing the single Triassic species (*Equisetosporites chinleana*) states that the spore is spherical, has two tightly wrapped elaters, and that the fossil cannot be distinguished from spores of the modern genus *Equisetum*. Also, he states that the spore case (coat) is thin and the spore is 36 microns in diameter.

All previously known spores of Paleozoic equisetacean plants are apparently without elaters regardless of the type of material studied. Hartung (1933) studied numerous calamarians, and their spores are likewise without elaters.

Maceration studies of Paleozoic coal have revealed many thin-walled transparent or translucent, spherical and sub-spherical spores that appear to have a

\* Contributions from the Science Laboratories of Coe College. No. 9 N. S. This study was made with the aid of a grant from the American Association for the Advancement of Science.

calamarian affinity. Knox (1938) has suggested such a relationship. These spores lack elaters and those forms which the writer has seen do not resemble the elater-bearing spores under consideration.

### Materials and Method

The coal ball from which the elater-bearing spores were secured was collected in an abandoned strip mine belonging to the What Cheer Clay Products Company, at What Cheer, Keokuk County, Iowa. The coal and associate shales are of Des Moines age in the Pennsylvanian System. The stratigraphic position of the What Cheer coal is not definitely known, but appears to be rather low in the Des Moines Series.

The coal balls of this mine are largely pyrite in composition, though many are also of the calcareous type. The particular individual described here is of the latter type and contains a wealth of leaves, stems, and seeds belonging to *Cordaites*, *Cordiaanthus*, *Cardiocarpon*, *Sphenophyllum*, *Lepidophyllum*, and much unidentified material. The coal ball is approximately five inches long, three inches wide, and five inches thick.

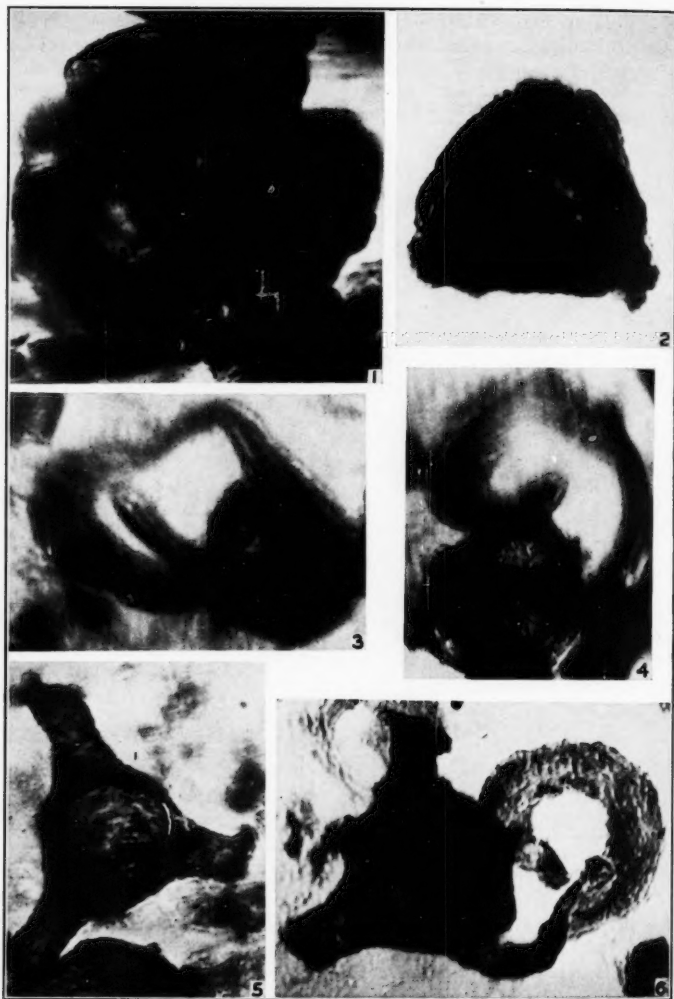
The spores occur in several loose masses associated with poorly preserved tissues that may be sporange remnants. Spores also occur scattered throughout the coal ball. Many more elaters than spores are to be found in the mass and most of the spores possess fewer than three complete elaters. It appears as though the same fragile nature of elaters existed in the Paleozoic as at the present time in the genus *Equisetum*.

Nitrocellulose peels were prepared after the method described by Graham (1933). The etching of the coal ball was accomplished by continued application of a very weak hydrochloric acid, until the carbonaceous material appeared about one hundred microns in relief.

### Description of the Spores and Discussion

Several thousand fossil spores and fragments were studied. These indicate that the usual shape of the spore is spherical, although many are slightly angular. The average diameter of the spores is approximately seventy microns including the perispore of coiled elaters. When the perispore coat is unrolled or shed, the endospore is approximately sixty microns in diameter.

The perispore coat consists of three circinately coiled elaters which remain attached to the endospore (Figs. 3, 4, 6). The place of attachment is the distal side of the spore since it is opposite the trilete mark on the endospore. The elaters are attached to a triangular portion of perispore which covers approximately one-sixteenth to one-twelfth of the surface of the endospore (Figs. 2, 3, 5). Frequently this triangular region extends out from the surface of the endospore and appears as a conspicuous base upon which the endospore rests (Fig. 5). The elaters are circinately coiled all in the same direction. The coil consists of approximately one and one-half turns. In this manner each elater including a portion of the triangular attachment area covers one-third of the endospore



Figs. 1-6. *Elaterites triferens*.—1. Three spores remaining in a tetrad group. The fourth spore and a portion of uppermost was removed by grinding, and thus revealing the trilete commissure on the proximal surface of the endospore. Slide No. 278P. — 2. A distal view of a single spore removed from a tetrad, the elaters are tightly wrapped and lying on the endospore which is visible beneath the translucent elaters. The triangular attachment area of the elaters is shown by a dark outline. Slide No. 280P. — 3. Distal

surface and contact is made with adjoining elaters at 120 degree angles. The contact of the elaters results in a trilete mark which resembles the commissure on the inner spore coat. Each elater averages about 177 microns in length, about 20 microns in greatest width, and about 5 microns in thickness. The tips are somewhat tapered and the central part of the elater is wider and more angular than any other portion. The elaters when extended remain in an open circinate coil and they are frequently flat or only slightly twisted near the points of attachment (Figs. 3, 4, 6). The elaters are translucent, yellow in color, and their surfaces are rugose or wrinkled.

The endospore has a medium thick wall, which is frequently wrinkled. The color of the wall is usually light brown and the wall is only slightly translucent. A trilete aperture is apparent in the best preserved spores (Figs. 1, 4). The rays of the commissure extend approximately one-third of the distance from their junction to the point of elater attachment.

The following points are important in a comparison of the above description with modern *Equisetum* spores. The diameter of *Equisetum* spores without elaters is approximately thirty microns, which is approximately one-half the diameter of the Paleozoic fossils here described. *Equisetum* spores possess four instead of three elaters and the manner of investing the spore is fundamentally different. According to Eames (1936) the elaters of *Equisetum* wrap spirally around the spore whereas the fossil elaters described in this paper are disposed in a circinate coil. The coiling of the elaters in the Triassic *Equisetosporites* is apparently like that of the modern genus since Daugherty (l. c.) states that the spores cannot be distinguished from those of the modern genus *Equisetum*. The elater tips in *Equisetum* are spatulate or spoon-shaped instead of tapered. In width and thickness *Equisetum* elaters are considerably narrower and thinner. Seldom do they remain flat except at the spatulate ends. *Equisetum* elaters are often thread-like due to their twisted condition.

No modern *Equisetum* spores has been recorded as having a trilete mark on the endospore wall, but the Mesozoic forms described by Halle (1908) as equisetacean, possess such marks. It appears, then, that the Mesozoic forms of the family resemble in this respect more closely the Paleozoic fossils than the modern species.

A question of affinity naturally arises for the Paleozoic elater-bearing spores, but at present this cannot be satisfactorily settled. However, no other known plants, fossil or living, except the Equisetaceae are known to possess elaters attached to the spores. Therefore it seems justifiable to assume that the fossil spores belong in the order Equisetales. As is evident from the above descrip-

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view of spore showing the triangular area to which the elaters are attached. Slide No. 281P. — 4. Proximal view of spore showing the trilete commissure, wrinkled nature of the endospore wall, and a circinately coiled elater. Slide No. 282P (cotype). — 5. Spore showing portions of three elaters and triangular attachment area beneath on the distal side of endospore. Slide No. 283P. — 6. Spore with uncoiled circinate elater. Slide No. 284P (cotype).

tion, the spores certainly differ enough morphologically from the spores of modern *Equisetum* to prevent their assignment to that genus. The Paleozoic and Mesozoic equisetaleans consist of the genera *Calamites*, *Archaeocalamites*, *Schizoneura*, *Phyllothea*, and *Equisetites*. The first two genera are classed in the Calamariaceae and the last three are usually considered as belonging to the Equisetaceae.

On the basis of Hartung's work (1933) the spores of *Calamites* apparently lacked elaters, and therefore the fossil spores in question cannot be considered as being closely related to them.

*Archaeocalamites* is not nearly as well known structurally as the former genus and occurs lower down in the Paleozoic rocks than the Des Moines Series. Nevertheless it possessed a cone that resembles those of the Equisetaceae more than those of *Calamites*. No spores are known to have been described for *Archaeocalamites*.

*Schizoneura* is best known from the Permo-Carboniferous and Triassic rocks of Europe and the Lower Gondwana Series of India. Its fertile shoots are unknown.

*Phyllothea* is known from the Permian, Triassic, and Jurassic rocks. It differs from modern *Equisetum* in the character of its leaves and sporophylls. No spores are known to have been described for this genus.

*Equisetites* is a genus of imperfectly known *Equisetum*-like fossil plants from the Carboniferous Period and the Mesozoic Era. These fossils bear close resemblance to *Equisetum*, but because they cannot be definitely assigned, are retained in a separate genus. Spores belonging to the genus *Equisetites* have been studied by Halle, but as stated above, they cannot be compared closely with the What Cheer material since they lack elaters.

The elater-bearing spores of What Cheer are apparently most closely related to the equisetacean genera *Equisetites*, *Phyllothea*, and *Schizoneura*. Since closer determination is impossible, and because the spore genus *Equisetosporites* of Daugherty by definition excludes the equisetalean spores of the What Cheer material, it is desirable to describe the latter under a new genus (see the following diagnoses).

#### *Elaterites* gen. nov.

Spores radially symmetrical; elaters three, derived from perispore, circumately coiled, nearly flat and only partly extended when unrolled; surface smooth or rugose, color yellow, translucent; when coiled, each elater covers approximately  $\frac{5}{16}$  of the endospore surface; attachment area triangular, approximately  $\frac{1}{16}$  to  $\frac{1}{12}$  of the spore surface; endospore spherical or subspherical; approximate diameter 60 microns; color light brown, slightly translucent; wall medium thick, smooth or wrinkled; trilete mark simple, proximal in position, rays extend  $\frac{1}{3}$  distance from junction point to elater attachment.

*Elaterites triferens* sp. nov.

General description as for genus; diameter 65-70 microns including investing elaters, 58-60 microns without; elaters 170-177 microns long, 17-20 microns wide, 4-5 microns thick.

Cotypes: Slides Nos. 282P & 284P in collection of L. R. Wilson. What Cheer Clay Products Company pit, What Cheer, Keokuk County, Iowa. Des Moines Series, Pennsylvanian System.

## Summary

1. Spores bearing elaters have been found in the Des Moines Series of the Pennsylvanian strata of Iowa. The discovery extends the geological range of this spore type from the Triassic Period back into the Pennsylvanian Period.

2. The spores are approximately sixty microns in diameter, have three circinate coiled elaters, and a trilete commissure on the endospore.

3. The phylogenetic affinity of the elater-bearing spores is assumed to be equisetalean, since that group alone has elaters attached to the spores.

4. Because the fossils differ morphologically from known spores they are assigned to a new genus. *Elaterites* is proposed to include these and similar fossil spores. All specimens here described are ascribed to *E. triferens*.

The writer wishes to thank Dr. C. A. Arnold and Dr. Th. Just for reading and criticizing the manuscript.

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## Notes and Discussion

### The Type of *Saxifraga pensylvanica* L., ssp. interior, ssp. nov.

George W. Burns

In a recent paper on "The Taxonomy and Cytology of *Saxifraga pensylvanica* L. and Related Forms" (Amer. Midl. Nat. 28: 127-160. 1942), designation of the type for *S. pensylvanica* L., ssp. interior ssp. nov. was inadvertently omitted. Therefore, the type of *S. pensylvanica* L., ssp. interior ssp. nov. is herewith designated as Arthur, Baily and Holway, July 23, 1886, St. Louis River (St. Louis Co.), Minnesota (University of Minnesota Herbarium, sheet number 178423). This is also the type of *S. pensylvanica* L., ssp. interior ssp. nov., var. *crassicarpa* (Johnson) comb. nov., and the name *S. pensylvanica* L., ssp. interior ssp. nov. thus rests on *S. crassicarpa* Johnson (Minn. Stud. Pl. Sci. 4: 43. 1923).

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### Note on "The Mating Types of Double Animals in *Euplotes patella*"

Mention of the instance of "cytogamy" described in *Paramecium bursaria* (Chen, T. T., 1940. Conjugation in *Paramecium bursaria* between animals with diverse nuclear constitutions. Journal of Heredity 31:185-196) was inadvertently omitted from my paper on page 190 (Amer. Midl. Nat. 30:175-195, 1943). In his paper Chen gives clear cytological evidence of the autogamous union of the pronuclei produced by one member of a conjugating pair.

The author wishes also to call attention to the fact that the word "not" in line 7, page 183, must be deleted in order that the sentence be a correct statement.—E. LAWRENCE POWERS, JR.

## Book Reviews

STRATIGRAPHY OF EASTERN AND CENTRAL UNITED STATES. By Charles Schuchert. John Wiley and Sons, New York, N. Y., 1943. 6 × 9 inches, xvii + 1013 pp., 4 pls., 78 correlation charts, 123 text figs., cloth, \$15.

This is the second volume\* in the great three-volume treatise on North American stratigraphy which, late in life, Professor Schuchert set himself to compile. Thanks to blessed longevity and an ageless mind, the task was largely completed before his death last Winter. It will in all probability prove to be our richest legacy from our greatest master of historical geology.

It was the original plan, according to the prefatory remarks, that the second volume should cover the historical geology of North America. As the work progressed, it became clear to him that however compactly he might crowd the data, no two covers could conveniently contain them. Realist that he was, it soon became manifest also that time would not be his to complete the survey. He leaves to his successors the enormous task of doing for the western reaches what he so superbly accomplishes for the eastern and central states of the Union. The remainder of eastern North America will be surveyed in a posthumous volume.

The present work opens with a ten-page historical essay on stratigraphic and chronologic classifications. Although fully cognizant of the current chaos in these aspects of historical geology, Schuchert was undoubtedly wise in refraining from introducing a remedy, as was his first inclination. In most instances he adheres to the rules of the Stratigraphic Code and the usage of the United States Geologic Survey. It is a surety, however, that until more drastic steps are taken along the line of a non-duplicative system of lithic and time nomenclature, and until strict recognition of the rule of priority prevails, we will continue to wander in chaos. In keeping with his usual progressive outlook, Schuchert adopts the time category *chron* to correlate with the lithic category *group*, and adheres, against the tide of American custom, to the international usage of the time unit *age* as a correlate of the lithic *stage*.

Both for convenience and genetic considerations, the book is divided into 8 unequal parts through which 33 chapters, in addition to the introduction, are distributed. Of 971 pages of text, 106 are devoted to Part 1, the New York standard Paleozoic section. Since the 31 states dealt with have one of the fullest Paleozoic records known, this is the main theme of the great book, and the seemingly disproportionate space devoted to New York is both geologically and historically most necessary. Part 2 deals with the "states athwart the Appalachian geosyncline" and embraces 9 state chapters. The relative development of the Paleozoic systems and of our knowledge of them in the various states is intimated by the pages required for Schuchert's epitome. Pennsylvania heads the list with 71 pages required to tell the bare facts of its magnificent record. New Jersey requires 16 pages; Maryland, 33; Virginia, 28; West Virginia, 24; eastern Tennessee, 33; North and South Carolina, 7; Georgia, 9 and Alabama-Mississippi, 19.

The Atlantic Coastal Plain is considered in Part 3 (99 pages). 12 pages are allotted to a general, and one cannot but feel all too brief, discussion of such challenging topics as the origin of the topography on the continental shelf, the nature and origin of coastal terraces and coastal plain deposits, and the structural history of the coastal

\* The first volume, *Historical Geology of the Antillean-Caribbean Region*, appeared in 1935. The last volume is promised in the introduction to the second one, and fortunately, it was largely completed at the time of Professor Schuchert's death last winter. It will complete the survey of eastern North America.

plain belt. The remainder of this part is given to sectional analysis of the province. Relatively little is said about the northeastern section, where to be sure the plain is poorly developed; but the current omissions may be reserved intentionally for the final volume which will deal more extensively with this area. Respectively 25 and 48 pages are given to the middle and southeastern coastal plain section. Florida receives somewhat more fullsome treatment than any other state in the province. Since the Gulf coast was rather fully considered in the first volume of the series, it has been omitted in the present volume.

Part 4 (131 pages) reverts to the Paleozoic theme which dominates the work. Five state chapters are grouped here because of the community of their history to the belt of Nashville-Cincinnati uplift. Try though he will, Professor Schuchert is unable to give a wholly integrated picture. The artificial limitations of nomenclature as a result of political boundaries, as well as unequal research in the states involved, must always stand in the way of synthesis. In this part, central and west Tennessee require 35 pages; Kentucky, 38; Ohio, 36; Indiana, 20 (seemingly too few); and Michigan 24. Similar semi-integrated treatment is given the states around the Ozark dome in Part 5 (94 pages). The states thus treated are Illinois (31 pages), Missouri (40 pages), and Iowa (23 pages). Arkansas and Oklahoma, which naturally belong here in part, are discussed elsewhere because of their relationship as well to the orogenic belt to the south.

Two chapters on Minnesota and Wisconsin comprise Part 6 (39 pages). Considering their importance, their treatment is rather brief, though no essential details appear to be omitted. In Part 7, the eastern Plains States, (76 pages) the picture shifts temporarily to the interior Mesozoic and Cenozoic relationships. Obviously, to discuss these political areas without considering the relations in the High Plains or the Rocky Mountains is a sad omission, of which nobody was better aware than Professor Schuchert,—but, alas, time was running out!

The states to the north and west of the borderland mass of Llanoria are taken up in Part 8 (155 pages). This completes the Appalachian Paleozoic history, in so far as it is known, from Pennsylvania to west Texas. Arkansas comes in for 26 pages and Oklahoma for 24. Texas receives extended treatment (72 pages) compatible with its size and importance.

The text is an admixture of compact listings of physical and biotic formational data and almost a prolixity of direct literature quotes. Especially considering the availability of Wilmarth's *Lexicon of Geologic Names* with its source quotations, this procedure seems unnecessarily to have increased the bulk of the series. The assiduity with which Professor Schuchert worked can be judged not only in the thousands of author citations, but also in the considerable bulk of new and clarifying information solicited personally from many sources. The epitomous result of this method of work is a compendium so packed with precise knowledge, and for the most part so unleavened by discussion or elaboration, that only the professional geologist (for whom it was exclusively prepared) will be competent, or diligent, enough to make fullest use of it. This is in no sense a criticism of the book, or especially of the series of which the book is an integral part, for Professor Schuchert has eminently succeeded in his primary purpose of amassing, for the first time, the basic data of American earth history. It should be noted in passing that Professor Schuchert intentionally omits consideration of both the Cryptozoic and the Pleistocene. It cannot be considered a fault that he does little weighing or choosing and is seldom critical in the text of this book. That privilege was apparently reserved for the closing chapters of the last volume.

Interspersed through the text are 79 correlation charts which are in some respects the most valuable and also most challenging part of the present volume. In these Professor Schuchert has occasionally ventured more of his keen insight and interpretive genius than is his usual wont in the text. Perhaps in his zeal to keep the bulk of the printed work within bounds, he may have sinned a bit on the side of omission of significant illustrations. The 123 line-cut text figures, few, if any, of which are original,

have been judiciously chosen; but rather long stretches of desert text are without this relief, even where illustrative material, in every way comparable to that employed, is readily accessible. Fortunately, we are spared the usual expensive and all too often meaningless photographs of rock-sections with which so many modern stratigraphic opera are cluttered. It is good to have several portrait plates of the founders of stratigraphic science in America, but the overcrowded plates have about as much esthetic appeal as the usual illustration of fossils.

Since the sciences of historical geology are at best adolescent, much progress lies ahead, and this will mean oftentimes disharmony with the present and the past. Even now, specialists can (and probably will) take exceptions to many matters of correlations in the present volume. But, such is progress. Every branch of geology is, and must long remain, in deep debt for the great service Professor Schuchert has done us.

In many respects the final volume, which is yet to appear, should prove to be most valuable and stimulating, for therein Professor Schuchert promises those philosophic and interpretative considerations, purposely largely omitted from the first two volumes, for which he was so peculiarly fitted. In this connection, historical geologists avidly await the paleogeographic maps over which Professor Schuchert had worked for so many years and in the compilation of which the data for the present series were assembled, and in the formulating of which he became the principal creator of a new science: paleogeography.

In this work, as in everything he wrote, we must all admire the questing, plastic, youthful mind to which Truth alone was worth defending. This is no book of superannuation or doddering retrospect. It is progressive and constructively modern.—KENNETH E. CASTER, University of Cincinnati.

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THE ROSEATE SPOONBILL. By Robert Porter Allen. Research Report No. 2 of the National Audubon Society, New York. xviii + 142 pp., colored frontispiece, 20 plates, 44 figs. \$2.50.

The preparation of a monograph on the Roseate Spoonbill took twenty-five months of concentrated study by a person already familiar with the bird and problems connected with its protection. The hope of the author was that the report would "help to clarify the problem of restoration of the Roseate Spoonbill as a common breeder in Florida and serve to arouse new interest in its future welfare throughout its range. It seems obvious that more research, much careful planning and, above all, a program of cooperative effort with certain of our neighbors to the south must be undertaken if the Spoonbill is to be permanently maintained as a nesting bird in our Gulf states." The contents appear to provide good grounds for these statements.

A long list of contributors as well as the thorough work of the author in the field brought many kinds of evidence not usually found in a report on so difficult a topic. The eight subtopics covered are distribution, abundance, migration and postnuptial wanderings, limiting factors, breeding-cycle behavior, food and feeding habits, plumages and molts, and the future. The time allotted could not permit the gathering of adequate evidence for all these topics. Discussion of the food and of the effects of parasites would have been better if based on more evidence or closer attention to the evidence. The discussion of parasites needs a determination of identity not difficult to make. Through most of the book, however, it is clear that enthusiasm in the field has been followed by equally persistent and energetic study to detect true significance of the facts.

Maps, charts, diagrams, and drawings of other kinds are nearly as important as the text in presenting the story of this bird. Sketches showing postures and positions assumed in the nesting behavior are especially instructive. Also, they do not have the heavy lines which are somewhat disturbing on some of the charts.

Both of the Research Reports show the beneficial results of careful editorial plan-

ning and arrangement such as can be obtained by the use of institutional facilities. They do not, however, show signs that a routine pattern has been established that will prescribe the content of future members. We anticipate that this series will come to be considered as an accomplishment of most permanent value among those of the National Audubon Society.—JEAN M. LINDSALE.

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PLANT ECOLOGY. By W. B. McDougall. Lea & Febiger, Philadelphia, 1941. Third edition, 285 pp., frontispiece, 118 figs. \$3.00.

Judging by the number of editions this textbook is apparently widely used and well liked. But is it the best possible cross section of current ecological knowledge which a student could get?

Ecology like many other biological sciences is at the moment in a state of flux and many of its time-honored concepts are now being subjected to critical study with new methods and often in an entirely new light. Neither these changes nor the numerous interrelations with other biological fields, notably taxonomy, genetics, and paleobotany, are clearly indicated despite the author's emphasis on the biological aspects of ecology. Would it not be profitable to record the value and results of transplant studies, of experimental ecology, and of the history of vegetation at least as far as it is necessary for a better understanding of present distribution? Or is plant ecology destined to remain stationary, while animal ecology progresses far beyond the attainments of its former preceptor?

These questions could be asked equally well of the authors of some other textbooks. In other words, is the status of plant ecology properly reflected in existing textbooks or is the interested student dependent on wide collateral, but frequently confusing reading? Unfortunately the latter is the case. Part of this difficulty is undoubtedly inherent in the subject, whereas the remainder is probably the result of our unwillingness to face the situation and to distill the mass of data for the sake of clarity. But by doing so a new ecology would emerge which would be equal to other leading biological sciences and which would contribute immensely to scientific knowledge in general and to the solution of many of humanity's present ills.—THEO. JUST.

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ECOLOGICAL CROP GEOGRAPHY. By Karl H. W. Klages. Macmillan Company, New York, 1942. xviii + 615 pp., 66 tables, 108 figs. \$4.50.

As the world must take inventory of its available food supply, this book makes its appearance at the right moment and for the greatest benefit of those in need of this information. Fortunately the outlook of the author is broad, a fact which greatly enhances the usefulness of the book.

By comparison with general textbooks of plant ecology the treatment of ecological factors is definitely more modern and refreshingly geographical in character. The many ramifications of *Ecological Crop Geography* and its relations to Man are fully and clearly set forth. The book is thus a dependable source of information on the major crops and their ecological behavior, distribution, yields etc.

One weakness must, however, be pointed out. Although many crop plants have for years been studied genetically, this is not apparent from the book. The interested reader will deplore the absence of adequate discussions of the influences of genetical and ecological factors, of the important contributions of the Russian school under the leadership of N. I. Vavilov, and of such pertinent works as E. Schieman's "Entstehung der Kulturpflanzen" and A. De Candolle's "Origine des plantes cultivées." But this is the only serious shortcoming of an otherwise well prepared and excellently printed book.—THEO. JUST.

